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Research Article

Keywords:

Posted Date: April 17th, 2026

DOI: <https://doi.org/10.21203/rs.3.rs-9426929/v1>

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Additional Declarations: No competing interests reported.

From coral reefs to gorgonian forests: Shared cues and hierarchical settlement in a temperate octocoral (*Paramuricea* sp.)

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ABSTRACT

Larval settlement is a critical bottleneck in coral life cycles, yet mechanistic understanding is largely derived from tropical scleractinians, however lacking for non-tropical octocorals. Tropical crustose coralline algae (CCA) and their associated microbiome are known to be a major trigger for settlement processes. We investigated settlement drivers in a temperate octocoral (*Paramuricea* sp.) to assess whether similar processes operate in temperate and cold-water coral forests: (1) In a choice experiment larvae were exposed to different types of substrates. Settlement occurred exclusively on substrates naturally colonized by crustose coralline algae (CCA), independent of rock lithology, indicating that biogenic surface properties, rather than mineral composition, govern settlement. Substrate covered with *Lithophyllaceae*-associated CCA induced settlement across depth ranges, whereas other CCA taxa and bare fragments did not. (2) Experimental exposure to the bacterial metabolite cycloprodigiosin (CYPRO) triggered settlement behaviour in up to 44% of the exposed larvae, suggesting chemical cues as primary inducers. (3) Spatial analyses of settlement patterns revealed that attachment rarely occurred directly on CCA surfaces. Instead, larvae settled near CCA and within millimetre-scale crevices and depressions. Small-scale heterogeneity suggests that microtopographic features act as secondary filters after chemical induction.

These findings indicate that key elements of settlement regulation might be shared between tropical reefs and temperate coral forests highlighting the joint importance of CCA communities and structural complexity for recruitment and conservation.

INTRODUCTION

Coral forests are among the most structurally complex marine ecosystems in temperate regions and represent important biodiversity hotspots, providing feeding, breeding, and nursery habitats for numerous marine organisms (Cau et al. 2020; Chimienti 2020; Hoarau et al. 2025). Their complex three-dimensional structure is formed by habitat-building gorgonians, which contribute substantially to ecosystem functioning and biological diversity (Colletti et al. 2025; Orejas et al. 2022; Ponti et al. 2018). Despite their ecological importance, temperate coral ecosystems have historically received less attention than tropical reefs, although their associated biodiversity can be comparable in many cases (Bongiorni et al. 2010; Freiwald 2003; Paoli et al. 2015; Roberts et al. 2006). At the same time, these ecosystems are increasingly threatened by multiple anthropogenic stressors, including climate change, pollution, ocean acidification, and particularly destructive bottom-contact fishing practices, which can cause large-scale habitat degradation and the loss of habitat-forming corals (Bavestrello et al. 1998; Bramanti et al. 2023; Hall-Spencer et al. 2007; Hinz 2015; Piazzini et al. 2021; Ponti et al. 2014).

The ongoing loss of structural organisms has far-reaching consequences: the decline of habitat-forming species leads to substantial reductions in biodiversity and can ultimately result in the collapse of associated communities, with impacts that extend beyond individual reef systems and include the loss of essential ecosystem services (Coleman & Williams 2002; Ellison et al. 2005; Norse et al. 2005).

Because many temperate coral systems occur in mesophotic or deep environments that are difficult to access and monitor, ecological impacts are often detected only at late stages, and fundamental aspects of their biology remain poorly documented (Da Ros et al. 2019; Montseny et al. 2021; Ragnarsson et al. 2017). Only recently have these ecosystems been collectively recognized as Marine Animal Forests, which has increased scientific and political awareness of their ecological significance (Orejas et al. 2022; Rossi et al. 2017; Rossi et al. 2022).

Because many habitat-forming species of temperate and cold-water reefs are characterized by slow growth rates, long maturation times, low recruitment rates, and high mortality during early life stages, both during dispersal as propagules and after settlement as young recruits and juveniles, their natural recovery following physical disturbance is often severely limited (Andrews et al. 2002;

Andrews et al. 2009; Fava et al. 2010; Prouty et al. 2016; Roberts et al. 2006). In these long-lived, slow-growing species, population persistence and recovery depend disproportionately on successful reproduction, larval settlement, recruitment, and the survival of juveniles to reproductive maturity, as adult turnover is slow and generational replacement occurs over extended time scales (Bramanti et al. 2016; Garrabou & Harmelin 2002; Linares et al. 2007). Given the increasing pressure on these valuable ecosystems, successful settlement and recruitment processes are therefore particularly critical for maintaining populations and enabling recovery after disturbance (Bramanti et al. 2009; Bramanti et al. 2015). Consequently, improving our understanding of early life stages and recruitment dynamics is essential for developing effective conservation and management strategies (Giordano et al. 2026). Tropical coral reefs have been studied extensively, and key aspects of the biology, life cycle, and dispersal strategies of habitat-forming coral species are often well understood (Harrison & Wallace 1990; Harrison 2011; Kahng et al. 2011; Richmond & Hunter 1990). This knowledge has enabled the development of targeted conservation actions and restoration strategies (Boström-Einarsson et al. 2020; Chamberland et al. 2017; Doropoulos et al. 2019; Heyward et al. 2002; Plucer-Rosario & Randall 1987; Randall et al. 2020). The success of such interventions, however, critically depends among others on processes occurring during early life stages. In tropical systems, we know for many species how larval settlement, substrate selection, early ontogeny, and post-settlement survival and growth can shape population dynamics (Caley et al. 1996; Hughes & Tanner 2000; Ritson-Williams et al. 2010).

Settlement represents a decisive transition from the pelagic larval stage to the benthic lifestyle and constitutes a major demographic bottleneck (Doropoulos et al. 2016; Edmunds et al. 2018; Hunt & Scheibling 1997; Keough & Downes 1982). Consequently, understanding the mechanisms governing larval settlement choice is central to explaining patterns of population connectivity and resilience, also in non-tropical reef ecosystems (Cowen et al. 2007; Pineda et al. 2007). Settlement is not a random process but is driven by active exploration and selection of suitable substrates (Hadfield & Paul 2001; Kingsford et al. 2002). Numerous studies on tropical corals have shown that larvae respond to a combination of physical, chemical, and biological cues when selecting settlement sites (Hadfield & Paul 2001; Heyward & Negri 1999; Petersen et al. 2021a; Sneed et al. 2014).

Biogenic signals often produced by microorganisms assembled in bacterial biofilms or on crustose coralline algae (CCA) are known to play a key role in inducing larval settlement. Tetrabromopyrrole (TBP) and the red pigment cycloprodigiosin (CYPRO), produced by bacteria associated with CCAs, have been identified as settlement inducers for tropical scleractinian corals on a molecular level (Petersen et al. 2021a; Tebben et al. 2011). The mechanism of CYPRO was found to be light-driven (Petersen et al. 2023). Under light exposure, CYPRO degrades into reactive oxygen species (ROS),

whereas in the dark it remains stable. Larvae that absorb CYPRO in the dark begin to appear red and, when exposed to light, CYPRO degrades within their tissues, driving metamorphosis into a sessile recruit. The importance of the light environment aligns with studies showing the influence of substrate orientation, surface complexity, and microhabitat conditions on larval settlement preferences (Gómez-Lemos et al. 2018; Heyward & Negri 1999; Petersen et al. 2021b; Tebben et al. 2015). Substrate choice can have profound consequences for post-settlement survival by mediating exposure to predation, sedimentation, and environmental stress (Doropoulos et al. 2016; Martínez-Quintana et al. 2023).

Comparatively little is known about settlement processes and substrate preferences in temperate and cold-water corals. Many non-tropical corals, particularly azooxanthellate octocorals, differ fundamentally from tropical scleratinians in terms of nutritional physiology, developmental timing, and habitat requirements (Cocito et al. 2013; Ribes et al. 1999; Roberts et al. 2006). These differences suggest that settlement cues and preferences identified in tropical corals may not be readily transferred to non-tropical systems. The limited studies, however, showed that temperate octocorals also respond to cues linked to CCA from the family *Lithophyllacae*, similar to some tropical corals (Manea et al. 2025; Tebben et al. 2015; Wahab et al. 2023; Zelli et al. 2020), suggesting some of the same mechanisms may be preserved across systems. However, lack of empirical data on settlement behaviour in temperate habitat forming species still represents a significant knowledge gap.

In this study, we focus on the settlement behaviour of a purple cold-water gorgonian of the genus *Paramuricea* occurring off the southern coast of Portugal. This species was only recently distinguished from its closely related Mediterranean sister species *Paramuricea clavata*, and reproduces similarly to the latter by surface-brooding its offspring (Linares et al. 2008). We examine larval settlement preferences across different substrate types and microhabitat conditions to identify key cues influencing settlement choice. Additionally, we tested the effect of the CCA associated bacterial-derived settlement cue CYPRO, which was identified as a multispecies cue for larval settlement in tropical scleractinian corals (Fiegel et al. 2025). By elucidating the drivers of successful settlement in this mesophotic gorgonian, this work aims to improve our understanding of recruitment processes in temperate coral habitats and to provide a mechanistic basis for future conservation and management efforts.

MATERIAL & METHODS

Larvae used in the following experiments were obtained ex situ from colonies of the purple morphotype of *Paramuricea* sp., collected as fisheries by-catch near Cape St. Vincent (Sagres,

southern Portugal) prior to the predicted reproduction season, between early July and mid-August 2024. Colonies were transferred to and maintained in a 150-L indoor, temperature-controlled (15–16 °C), semi-closed seawater system at the Ramalhete Marine Station (CCMAR, Faro, Portugal). The tank room was illuminated with dim blue and green light following the natural daylight cycle (for exact collection locations and detailed maintenance conditions, see Egger et al. 2026). Because eggs, embryos, and larvae of this species are negatively buoyant, the propagules were collected daily during the spawning period by gently siphoning the tank bottom using a small hose. The collected propagules were transferred to 1L plastic containers and maintained in the same temperature-controlled room as the parent colonies. Gentle water movement was provided via aeration tubing, releasing a few air bubbles per second, and approximately two-thirds of the water volume was exchanged every other day.

Experiment 1: Substrate Choice

To evaluate whether larval settlement is substrate-specific and influenced by substrate origin (natural vs. artificial) and biological conditioning, six ecologically relevant substrates were selected.

Three substrates, brown sedimentary rocks (Mesozoic limestones/sandstones; Díez-Montes et al. 2025), dark volcanic rocks, and crustose coralline algae (CCA) fragments, were collected as fishing bycatch from 50–90 m depth near Cape St. Vincent, representing substrates naturally available in the habitat. Smaller pieces were obtained by splitting larger rocks and gently brushing the surface to remove soft biogenic overgrowth while preserving CCA.

To assess the effect of artificial substrates conditioned in situ, ceramic coral plugs (Ecotech Marine®) were deployed at ~130 m depth near the collection site for two months prior to the experiment. In addition, two substrates with distinct CCA assemblages were included to test the influence of origin and species composition: CCA-covered rocks from shallow water (3 m, Sagres) and CCA maintained under controlled conditions at the Ramalhete Marine Station.

CCA taxa were identified using DNA barcoding of the mitochondrial COI-5P marker following Saunders (2005). Sequences were compared to GenBank references using BLAST, and identifications were based on sequence similarity to published taxa.

The six substrate types differed in origin, depth, and CCA composition:

Substrate 1: Deep brown sedimentary rocks with CCA (50–90 m), including taxa related to *Lithophyllum nitorum* (96–97% identity) and *Lithothamnium/Boreolithothamnium* spp. (87–88%).

Substrate 2: Deep dark volcanic rocks with CCA (50–90 m), with taxa related to *Lithophyllum nitorum* (96–97% identity).

Substrate 3: Deep CCA fragment (50–90 m), without reliable species-level identification.

Substrate 4: Coral plugs incubated at depth (~50 m, Sagres) for two months, without CCA cover.

Substrate 5: Shallow rocks with CCA (3 m, Sagres), including *Lithophyllum artabricum* (98.2%) and *Lithophyllum incrustans* (100%).

Substrate 6: CCA from outdoor tanks at the Ramalhete Marine Station, related to *Harveyolithon* sp. (89%).

Settlement Choice Experiment

Three replicates of 100 purple larvae, collected from the tank between September 3rd and September 9th, 2024, were used to test substrate settlement choice. The larvae were placed in 2.15L oval containers and offered 2.17 to 14.13 cm² big pieces of each substrate on September 10th, 2024. The containers were provided with slow aeration to allow for a slight water mixture and kept in a 16° temperature-controlled room. Water temperature inside the basins was measured regularly and was slightly below the room temperature (14-15°). Every second day, 50% of the water was exchanged by fresh running seawater from the tank system kept at the same temperature. Larval settlement was checked daily from September 11th, 2024, onwards. Starting when the first settlement was observed on September 13th, 2024, settlers were also photographed daily, until no new settlers were recorded for three consecutive days (September 25th, 2024). When a substrate accumulated more than five settlers, the substrate was replaced with a unit of the same type to maintain the available settlement space and minimize potential effects of crowding or conspecific attraction on subsequent settlement choice.

Overall settlement preference among substrates

Overall settlement preference was quantified as the total number of settled larvae per substrate per container, summed across the experimental period. This metric represents cumulative settlement choice independent of post-settlement mortality and temporal variation in settlement rate. Substrate acceptance was further assessed as a binary response variable, indicating whether at least one larva settled on a given substrate within a replicate and observation period. For each substrate, the proportion of observations with settlement was calculated across all replicates and time points. Because several substrates showed complete absence of settlement (i.e. zero variance), statistical modelling was not appropriate, and results are reported descriptively.

Subsequent analyses therefore focused on settlement dynamics among the accepted substrates (1, 2, and 5)

Effect of time post substrate encounter on settlement preference

To test whether settlement dynamics changed with larval age, daily numbers of newly settled larvae were analysed using a negative binomial generalized linear mixed model (GLMM) to account for over dispersed count data. The number of newly settled larvae was modelled as a function of substrate and larval age, with larval age included as a nonlinear predictor using a natural spline (df = 2). Replicate was included as a random intercept. Analyses were restricted to substrates on which settlement occurred (substrates 1, 2, and 5). Pairwise differences among substrates were assessed using estimated marginal means with Benjamini–Hochberg correction for multiple comparisons. Model fit was assessed using simulated residual diagnostics. All analyses were performed in R (v4.4.1) using RStudio (v2024.12.1). Models were fitted using the glmmTMB package (v1.1.14), and diagnostics were conducted using DHARMa (v0.4.7).

Experiment 2: Cyclprodigiosin exposure

Settlement cue production

The settlement cue cycloprodigiosin (CYPRO) was produced as described in Petersen et al. (2021a). Briefly, *Pseudoalteromonas rubra* cultures were reactivated from a cryo culture stored at -80 °C and inoculated on Marine Broth (MB, Carl Roth GmbH) agar plates for 48 hours. A single colony was picked, transferred to an Erlenmeyer Flask with MB liquid media and placed on a shaker. After 24 hours, the clear yellowish media turned into a turbid state. In this state, 1mL of the liquid media was used per MB agar plate for the inoculation. Following a 24-hour incubation period at room temperature in the dark, the bacterial lawn was scraped from the agar surface and extracted with a mixture of 1:1 methanol (MeOH) ethyl acetate (EtOAc). The suspension was homogenized using an immersion blender (Ultra-Turrax T25, Janke & Kunkel IKA Labortechnik) at 12,000 rpm for 30 s and then placed for 10 s in an ultrasonic bath (Bandelin Sonorex). The resulting extract was filtered through a cellulose filter (grade 3 hw, sartorius) and the solvent was evaporated using a speedvac system (Christ, Gefriertrocknungsanlagen GmbH). The dried extract was dissolved in MeOH and further purified by liquid-liquid partitioning, C18-based solid-phase extraction (SPE, SUPELCO), and high-performance liquid chromatography with a semi-preparative C18-column and a diode array detector (HPLC-DAD, Agilent Technologies). The CYPRO quality was confirmed by ultrahigh resolution mass spectrometry. All steps were conducted under low light intensities to prevent degradation of the light-sensitive CYPRO compound.

Experimental set-up

Larvae were shipped from Portugal to Germany inside insulated stainless-steel vacuum flasks filled with seawater, to maintain temperature stability. They arrived with a water temperature of 19 °C, a salinity of 36.9 psu, and a pH of 8.0. For the experiment, a water mixture with 50% of the original water and 50% of artificial filtered sea water (AFSW, Pro Reef, Tropic Marin) was applied with a salinity of 36.1 psu and a pH of 8.29. The experiment was performed in an incubator (Certomat BS-T, B.Braun Sartorius) at 16°C. For illumination, an Ecotech Marine Radion XR15 was used at 2 $\mu\text{mol}/\text{m}^2/\text{s}$ with a peak at 450nm blue light). Larval settlement was followed in a 24-well plate with a total of 1.9 cm^2 well surface area. CYPPO dissolved in methanol (MeOH) with a concentration of 0.1mg mL^{-1} was pipetted into the individual wells to achieve the target final treatment concentrations [$\mu\text{g cm}^{-2}$]. After evaporation of the MeOH, 2.5mL of the above-mentioned water mix and three larvae were added to each well. Note that CYPPO concentrations are stated in $\mu\text{g cm}^{-2}$ due to the low water solubility of CYPPO. A negative control (NEG) treatment, containing only evaporated MeOH and two positive control treatments (POSI - Deep brown sedimentary rocks and POSII – shallow CCA (*Lithophyllum artabricum* or *Lithophyllum incrustans*) were additionally applied. All treatments were run in 3 well replicates. After 2, 5, and 9 days, an exchange of 2 mL of water volume using AFSW was applied. The experiment was monitored after 1, 2, 5 and 9 days. After 2 days, stable attachment was confirmed using a gentle pipette flow. pipette flow.

Statistical analysis

In experiment 2, only the difference in mean settlement percentage between the negative control (NEG) and the different CYPPO concentrations as well as the positive controls (POS) within each timepoint were of interest. Because these comparisons were defined as a priori based on the experimental hypothesis, we performed pairwise comparisons between the NEG and each treatment using Dunn's test ($\alpha = 0.05$) with Holm correction for multiple testing. To assess overall group differences, a non-parametric Kruskal–Wallis test was additionally conducted. However, since our primary objective was to test predefined contrasts between the NEG and the treatments, Dunn's tests were performed regardless of the significance of the global test. R (version 4.4.2) with the RStudio IDE (version 2024.9.1.394) was used for data analysis. The packages dunn.test (1.3.6) and tidyverse (2.0.0) were used for statistical testing, data manipulation, and plotting.

Experiment 3: Spatial settlement preferences

Study material and image acquisition

To investigate small-scale settlement preferences, we tested spatial clustering, preference or avoidance of CCA, settlement proximity to CCA, and preference or avoidance of crevices. The study material consisted of flat stones with varying crevice structures and CCA coverage, bearing coral settlers obtained from Experiment 1 and from additional settlement challenge assays. The stones were photographed using multiple overlapping frames under a Zeiss Stemi stereomicroscope equipped with an Axiocam camera at 8× magnification. Individual coral settlers were additionally imaged at 30× magnification to allow clear identification and precise localisation as discrete points on the stone surface. Only the exposed upper surface of each stone was considered for analysis, and stones that were not flat were excluded.

Image preprocessing

Images acquired at 8× magnification were merged using the Photomerge function in Adobe Photoshop (version 22.2), as it provided greater flexibility for manual correction than freeware alternatives, thus resulting in qualitatively comparable results. Settings were adjusted to allow only repositioning, without distorting individual images. Merged images were checked for quality, layers manually corrected if needed and excluded if not of sufficient quality (see also **Figure 1** for image processing workflow).

Coral settlers were then manually mapped on the photomosaics. To delineate living CCA from the remaining stone surface, the selective magenta colour channel was enhanced and manually edited as necessary. CCA areas were selected by colour and transferred to a new layer. Crevices, depressions, and holes were defined as regions of the stone surface that are lower in elevation relative to the surrounding surface, exhibiting a concave morphology and typically appearing shaded in the images. In the following context, these features are collectively referred to as crevices.

To extract crevice areas, image intensity levels were adjusted until these lower regions were selectively darkened. The resulting segmentation was manually refined to correct misclassifications and ensure accurate delineation of crevice boundaries. The extracted regions were then transferred to separate layers. All layers were resized as needed and exported as PNG files for downstream analysis in ImageJ (version 1.54g).

Digitalisation of settlement area, coral settlers and habitat

Digitisation and spatial analysis followed the workflow described by (Giordano et al. 2026). Spatial rescaling to millimetres was applied, and the outline of each settlement stone was manually delineated using the Polygon Selection Tool in ImageJ. Polygons followed the visible boundary of the

stone surface, excluding background and non-substrate areas, and represented the spatial observation window for subsequent point-pattern analyses. Polygon vertex coordinates were exported via the ROI Manager and saved as CSV files containing x–y coordinates. Individual coral settlers were visually identified and digitised by manually marking their centroid positions, with each settler recorded as a single point. The x–y coordinates of all settlers per stone were exported as CSV files. CCA-covered areas and crevice habitats were scaled, segmented into binary raster masks, and small isolated pixels were removed using particle analysis in ImageJ to reduce noise.

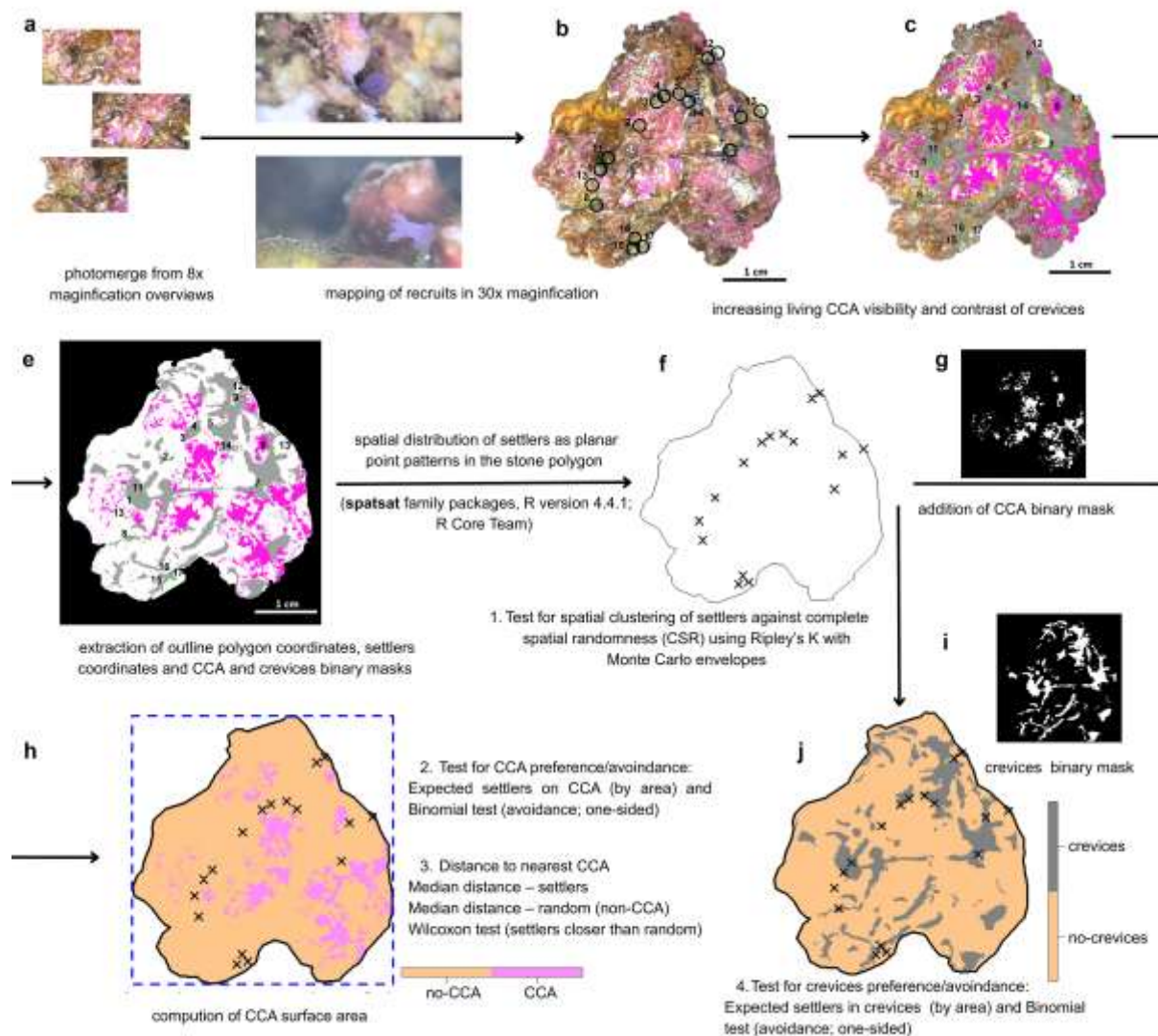


Figure 1 Workflow for quantification of settlement preferences of purple *Paramuricea* sp. larvae, including spatial clustering and micro-scale habitat selectivity. (a-j) indicating the order of steps.

Spatial data processing in R

All spatial analyses were conducted in RStudio IDE (v.2024.12.1, R v.4.4.1) using the spatstat package suite (v.3.5.0). Polygon outlines were imported and converted into spatial windows, and settlement locations were represented as spatial point patterns constrained to the stone surface.

Spatial clustering

Spatial clustering of settlers within individual stones was quantified using Ripley's K-function, which describes the expected number of neighbouring points within distance r of an arbitrary point (Ripley 1976). Observed K-functions were compared against simulated envelopes to assess significant departures from randomness, with edge effects corrected using the border correction method. For each stone, clustering strength was summarised as the integrated deviation of the border-corrected $K(r)$ from CSR:

$$\int_m^M [K(r) - \pi r^2] dr$$

for different M . For stone-scale analyses, the upper integration limit M was defined as one quarter and one third of the minimum stone diameter to minimise edge effects and ensure comparability across stones (Baddeley et al. 2015). To assess clustering at biologically relevant settlement scales, additional analyses were conducted using fixed integration limits of $M = 1, 2$, and 3 mm. These values were chosen based on observations that individual settlers were smaller than 1 mm in size and formed only small clusters within this spatial range. Larger distances (>3 mm) correspond to patterns more consistent with stone-scale clustering rather than local settler interactions. Although distances up to 5 mm were tested, no additional clustering was detected, supporting the selected range. Statistical significance was assessed using Monte-Carlo simulations of CSR (999 simulations), in which point patterns with the same number of settlers were simulated within the empirical stone outlines and clustering strength was recalculated for each simulation. The Monte-Carlo p-value was computed as the proportion of simulated clustering strengths at least as extreme as the observed (Baddeley et al. 2015).

CCA preference/avoidance

CCA masks were converted to binary spatial images and aligned to the sampling frame. CCA surface area was calculated as the proportion of stone area covered by CCA. Settlement locations were classified as occurring on CCA or non-CCA substrate. Settlement preference was evaluated using a use-availability framework (Manly et al. 2002), in which the expected number of settlers on CCA was calculated based on proportional CCA area. Observed and expected counts were compared using an exact binomial test. To assess consistency across stones, differences between observed and expected settlement on CCA were tested using a one-sided Wilcoxon signed-rank test. To assess

whether proximity to CCA was influenced by crevice availability and whether this relationship varied among stones, a linear mixed-effects model was fitted with distance to the nearest CCA as the response variable, crevice presence as a fixed effect, and stone identity as a random intercept:

Settlement proximity to CCA

Distances from each settler to the nearest CCA patch were calculated for each stone. As a null model, an equal number of random points was generated within each stone (restricted to non-CCA areas), and distances to the nearest CCA patch were computed (Baddeley et al. 2015). Median distances were compared between observed and random points per stone, and differences ($\Delta = \text{observed} - \text{expected}$) were tested against zero using a one-sided Wilcoxon signed-rank test.

Crevice preference/avoidance

Crevice area was quantified as the proportion of total stone surface. Observed settlement within crevices was compared to expectations based on area availability, and deviations were tested across stones using a one-sided Wilcoxon signed-rank test.

Dependence between CCA and crevices and effect of stone identity

Spatial associations between crevices and crustose coralline algae (CCA) were assessed by comparing binary raster maps on a per-pixel basis and quantifying their overlap within each stone.

To test whether crevices influenced proximity to CCA, distance to CCA was modelled as a function of crevice presence using a linear mixed-effects model with stone identity as a random intercept.

Variation in crevice use among stones was assessed using a binomial generalized linear mixed-effects model including stone identity as a random effect. Models were fitted in R using the lme4 package.

RESULTS

Settlement behaviour

First settlement following substrate encounter was observed after three days, consistent with our other observations (see Egger et al. 2026). Permanent settlement occurred only after larvae had intensively explored the substrate for several days ([Video 1](#), **Figure 2**) and repeatedly formed temporary, loose attachments (**Figure 2**, transparent colours). During this exploratory phase, larvae were observed crawling repeatedly over CCA (**Figure 2a, b**). They also actively probed the substrate by flattening their bodies against the surface, changing shape, then detaching and repeating this

behaviour elsewhere (Video 2; **Figure 2c**). This probing behaviour was most frequently observed in crevices and substrate depressions, where larvae were also found to accumulate (**Figure 2d**).

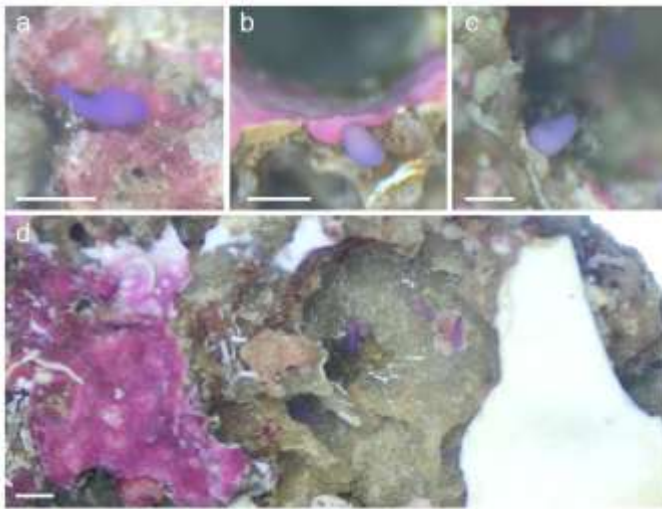
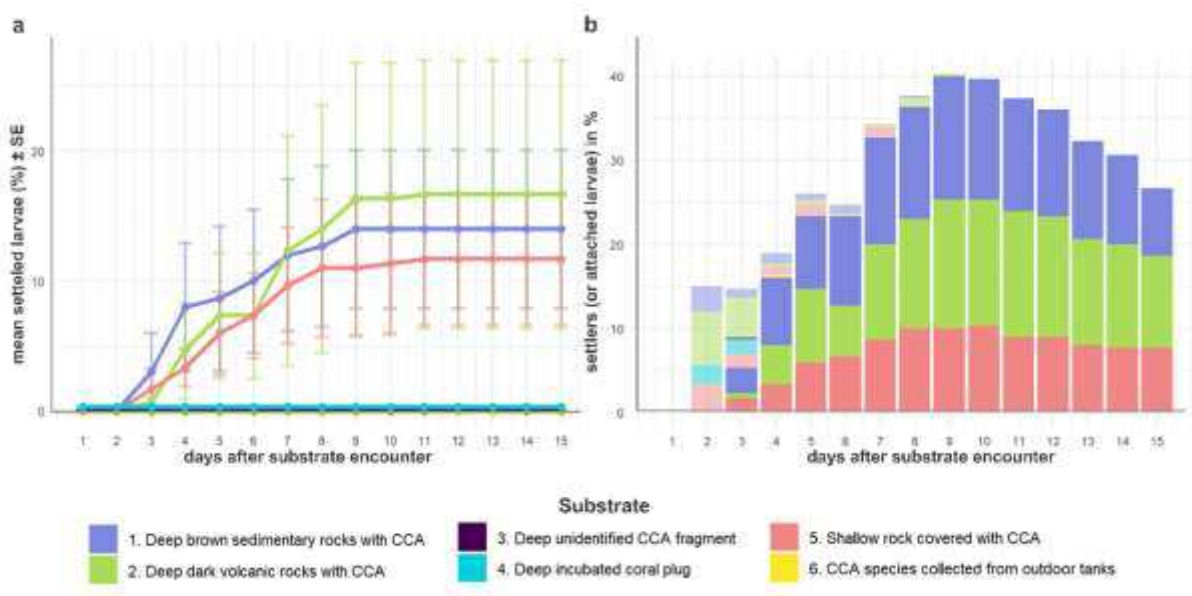


Figure 2 Larval probing behaviour of purple *Paramuricea* sp. following substrate encounter (a–c) Individual larvae (purple) observed on or next to crustose coralline algae-covered substrate, showing shape changing, flattening on the substrate, and loose and transient attachment. (d) Overview of a substrate patch with multiple larvae exploring and intermittently attaching in crevices and depressions prior to permanent settlement. Scale bars are 500µm.

Experiment 1: Substrate Choice

Larval settlement exhibited a clear binary pattern of substrate acceptance. No settlement was observed on substrates 3, 4, and 6 across any replicate or time point, indicating complete avoidance of these substrates. In contrast, settlement occurred on substrates 1, 2, and 5 with comparable probabilities (26.7–28.9%), suggesting that larvae did not strongly discriminate among these substrates at the level of settlement occurrence. Notably, all accepted substrates were natural rocky substrates bearing CCA: deep brown sedimentary rock with CCA (substrate 1), deep dark volcanic rock with CCA (substrate 2), and shallow CCA-covered rock (substrate 5), which supported settlement in all replicates (**Figure 3**).

Among the substrates that supported settlement (substrates 1, 2, and 5), the number of newly settled larvae was primarily driven by time rather than substrate identity. Settlement increased nonlinearly over time, as indicated by a significant effect of larval age (negative binomial GLMM, spline term: $p < 0.001$). In contrast, no significant differences in settlement intensity were detected among substrates (all pairwise comparisons, BH-adjusted $p \geq 0.77$). Variability among replicates was negligible, indicating consistent settlement patterns across experimental units.



398

399 **Figure 3 Substrate choice and settlement dynamics of *Paramuricea* sp. larvae.** (a) Mean cumulative percentage of larvae
 400 that settled on each of the six substrates over 15 days after substrate encounter (three replicates per substrate, N = 100
 401 larvae per replicate). (b). Total percentage of settlers recorded per day on each of the six substrates over the 15-day
 402 observation period. Transparent colours indicate larvae that remained attached but had not completed settlement. The
 403 figure also shows the subsequent fate of settled larvae over time. Note that there was no settlement observed on the
 404 substrates 3, 4 and 6.

405

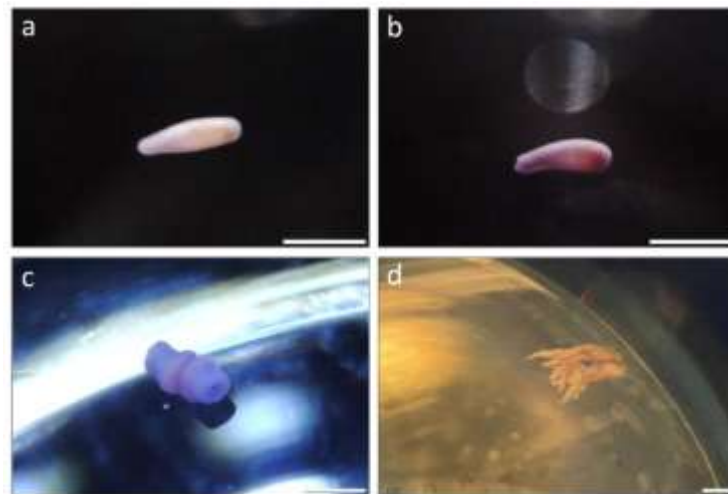
406 **Effect of larval age on settlement preference**

407 Larval age significantly affected settlement intensity, with settlement showing a nonlinear temporal
 408 pattern. In contrast, settlement did not differ among substrates, and temporal dynamics were
 409 consistent across substrates, indicating no evidence for age-dependent changes in substrate
 410 preference.

411 **Experiment 2: Settlement cue CYPRO**

412 *Paramuricea* sp. larvae (**Figure 4a**) visibly accumulated the red settlement cue CYPRO in their tissue
 413 and appeared red after an exposure of 12h (**Figure 4b**). *Paramuricea* sp. recruits settled in response

to CYPRO on the plastic surface of the well plate and developed similarly to those observed on



natural substrate (Figure 4c, d).

Figure 4 Larvae and recruits of *Paramuricea* sp., settled with CYPRO. (a) Swimming negative control larva that was not exposed to CYPRO. (b) Swimming larva after 12 hours exposure to the red pigment CYPRO. Both images were taken under the same illumination settings. The larva appears red due to the uptake of the red settlement cue CYPRO. (c) *Paramuricea* sp., recruits settled exposed to CYPRO after 5 days. (d) *Paramuricea* sp., recruits settled with CYPRO after 25 days of further development. Scale bars are 500µm.

Larvae settled in a concentration-dependent manner, exposed to a range of CYPRO concentrations (Figure 5). The highest larval settlement (mean $44.4 \pm 22.2\%$) was observed after 5 days at the highest applied concentration ($0.53 \mu\text{g cm}^{-2}$ CYPRO). No settlement was observed in the two lowest CYPRO concentrations (0.05 and $0.13 \mu\text{g cm}^{-2}$). Larvae exposed to $0.26 \mu\text{g cm}^{-2}$ CYPRO, settled after 9 days ($38.9 \pm 20.0\%$), and when exposed to $0.39 \mu\text{g cm}^{-2}$ CYPRO, $11.1 \pm 1\%$ of the larvae had settled by Day 5; however, these settlers had died after 9 days (Appendix Figure 8). Furthermore, no settlement was observed in the negative control (NEG), nor in the two applied positive controls (POS I and POS II). To analyse significant settlement reactions in CYPRO treatments, compared to the negative control per timepoint, first a global Kruskal-Wallis test was performed (day 2 - $\chi^2 = 14.6087$, $\text{df} = 7$, $p\text{-value} = 0.04$; day 5 - $\chi^2 = 9.977$, $\text{df} = 7$, $p\text{-value} = 0.19$ and day 9 - $\chi^2 = 13.746$, $\text{df} = 7$, $p\text{-value} = 0.06$). This was followed by pairwise Dunn tests, even if the Kruskal-Wallis test indicated no global significance. The pairwise Dunn test showed a significant difference between the NEG and $0.26 \mu\text{g cm}^{-2}$ CYPRO after 9 days (adjusted $p = 0.026$), NEG and $0.53 \mu\text{g cm}^{-2}$ CYPRO after 2 days (adjusted $p = 0.002$), after 5 days (adjusted $p = 0.031$) and after 9 days (adjusted $p = 0.026$).

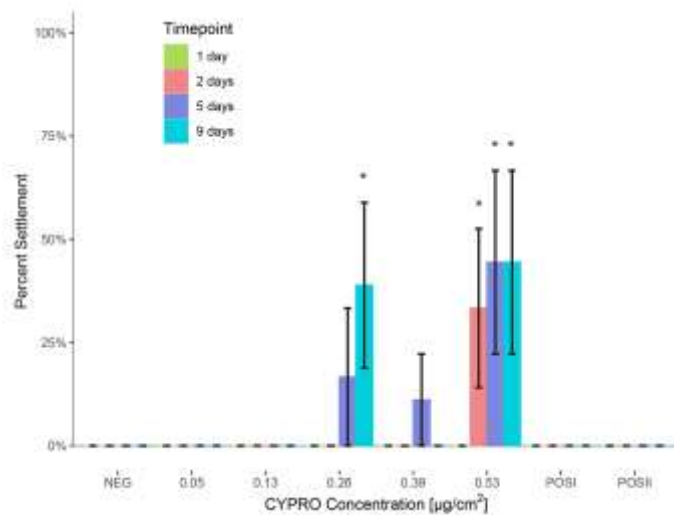


Figure 5 Settlement of *Paramuricea* sp larvae exposed to CYPRO. Mean number of larvae in [%] settled per CYPRO treatment in $\mu\text{g cm}^{-2}$, negative control (NEG) or positive control (POSI and POSII), monitored after 1,2,5 and 9 days experiment duration (3 replicates, N=3). Error bars display $\pm$ standard error. Asterix displays significant results ($p < 0.05$) compared to the NEG treatment.

Experiment 3: Spatial settlement preferences

Substrate preference

Settlers were occasionally observed to cluster in close proximity to one another (**Error! Reference source not found.** e). Although settlement directly on crustose coralline algae (CCA) was rare, settlers frequently occurred in close proximity to CCA (**Figure 6b,e**). Settlers were most commonly found within small and large crevices and substrate depressions (**Figure 6c,d**); however, in the

absence of nearby crevices, they also occurred on exposed substrate surfaces (**Figure 6a,e**).

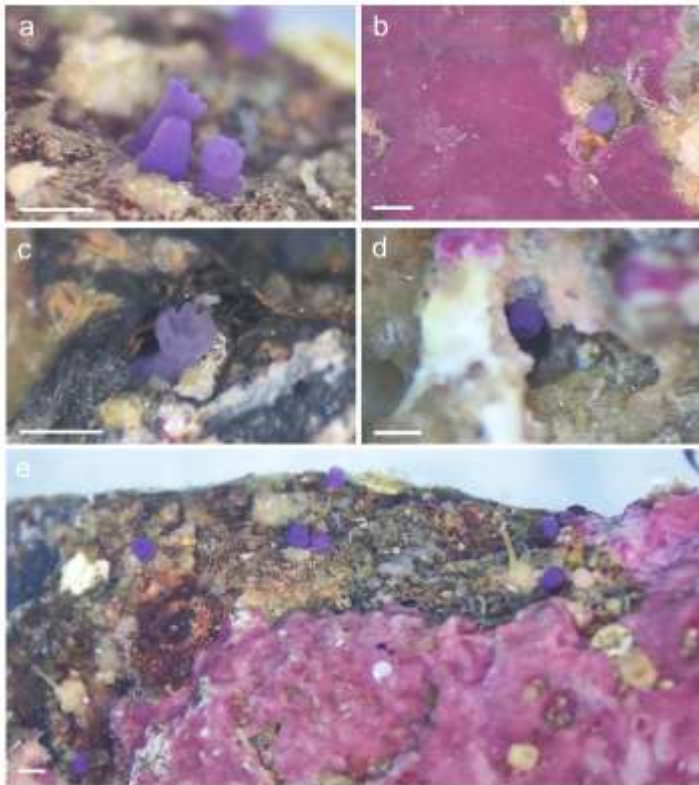


Figure 6 Spatial distribution and microhabitat use of settlers of *Paramuricea* sp. on experimental substrates. (a, e) Three Settlers near one another on exposed substrate surfaces. (b, e) Settler directly next to crustose coralline algae (CCA). (c, d) Settlers sitting in small and large crevices and substrate depressions. Scale bars are 500µm.

Spatial clustering

Spatial clustering of settlers varied strongly across all stones and was highly scale-dependent (**Figure 7 a, b** and Appendix **Table 6**).

When clustering strength was integrated over stone-scale distances ($\frac{1}{4}$ and $\frac{1}{3}$ of the minimum stone diameter), most stones showed no significant departure from complete spatial randomness (CSR).

Only one stone (PP03, **Figure 7b**) exhibited significant clustering at stone-scale distances, indicating aggregation extending beyond the immediate settlement scale (for p-values see Appendix **Table 6**).

In contrast, analyses at biologically relevant small spatial scales (1–3 mm) revealed substantial heterogeneity among stones. A subset of three stones (PP42, PP36, and PP28) exhibited statistically significant clustering at very small distances (≤ 2 mm), consistent with localized settlement aggregation, and three more stones (PP31, PP03, and PP22) showed a weak tendency of clustering at approximately 3 mm (**Figure 7a**). The remaining majority of eight stones showed no evidence of clustering at any scale, with spatial patterns indistinguishable from CSR in both the small-scale (1–3 mm) and stone-scale analyses. Several stones exhibited weak negative deviations of the K-function, but these were not statistically significant and therefore do not support consistent inhibition.

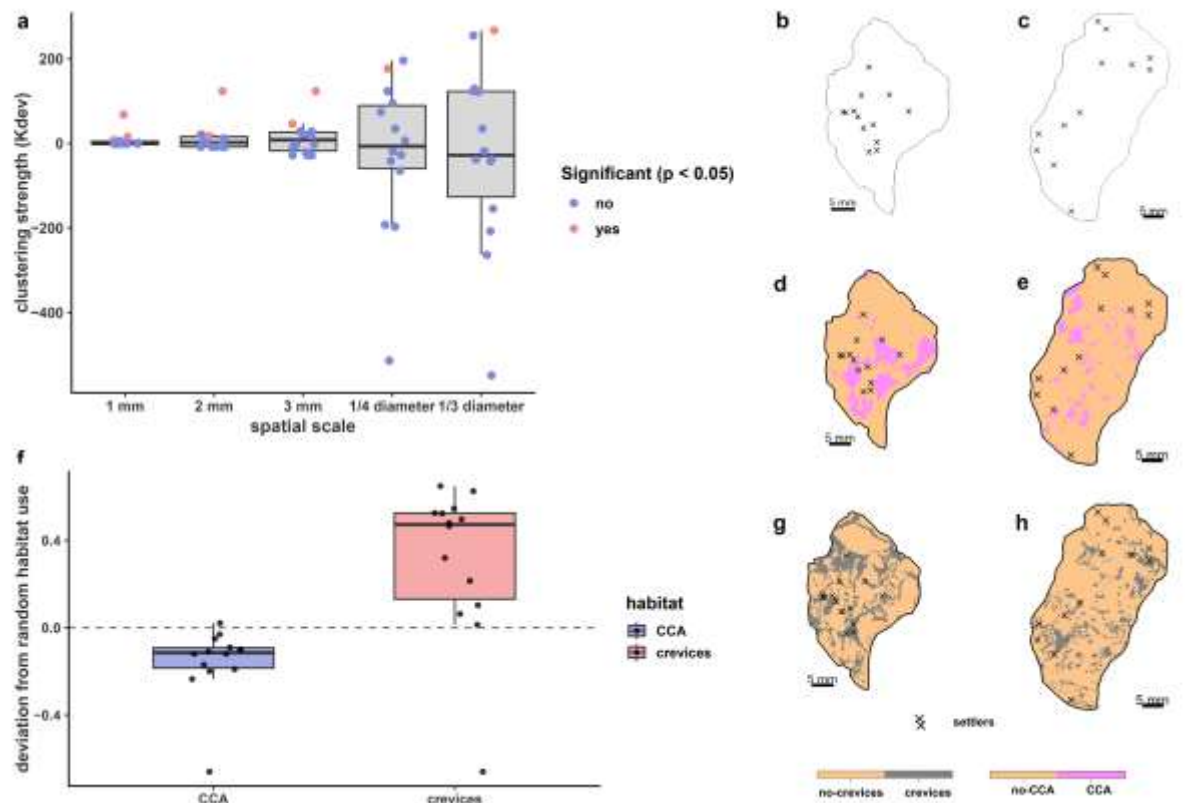


Figure 7 Spatial settlement patterns of *Paramuricea* sp. larvae on natural substrates with varying cover of crustose coralline algae (CCA) and crevices. (a) Distribution of clustering strength (K deviation) across spatial scales. Points represent individual stones and are coloured by statistical significance (Monte Carlo test, $p < 0.05$). (b, c) Representative examples of spatial distributions of settlers. (b) A clustered pattern at the stone scale ($\frac{1}{4}$ – $\frac{1}{3}$ of minimum diameter) with weak small-scale clustering, and (c) a random distribution with no clustering detected at any scale. (d, e) Spatial relationship between settlers and CCA, showing absence of settlement directly on CCA but reduced distances to CCA relative to random expectations. (f) Habitat-specific deviation from random settlement. Deviations between observed and expected habitat use are shown for CCA and crevices. Values below zero indicate avoidance relative to availability, while values above zero indicate preference. (g, h) Spatial relationship between settlers and crevices, showing disproportionately higher settlement within crevices than expected under random distribution. Results are shown for all stones (replicates; see Appendix Table 6).

Settlement in relation to CCA and crevices

Analysis of habitat overlap showed that crevices were predominantly located outside areas covered by CCA, with only a very small proportion of crevice area overlapping with CCA. This indicates that crevices and CCA are largely spatially independent habitat features.

CCA avoidance

Settlement on CCA surfaces was rare and was observed on only two stones (Table 6). Across stones, the observed number of settlers on CCA was consistently lower than expected based on CCA area alone (Figure 7 f) (Wilcoxon signed-rank test, $p < 0.001$), consistent with avoidance of CCA as a settlement substrate.

Settlement proximity to CCA

Despite this avoidance, settlers tended to occur slightly closer to CCA than expected by chance. The difference between median distances from settlers to the nearest CCA patch and from randomly placed points on non-CCA substrate (Δ median distance = settlers – random) ranged from –1.84 to 1.35 mm. Across stones, the median Δ distance was –0.20 mm (IQR = 1.26 mm). However, this tendency was not statistically significant (Wilcoxon signed-rank test, $V = 29$, $p = 0.077$; one-sided test) and substantial variation in settlement patterns was observed among stones. In the mixed-effects model, stone identity accounted for approximately 37% of the total variance in distance to CCA, indicating that proximity to CCA is strongly influenced by stone-specific characteristics. Crevice presence had a negative but non-significant effect on distance to CCA (estimate = –0.689, SE = 0.588, $t = -1.17$; **Table 7**), indicating that settlers located in crevices were not significantly closer to CCA than those outside crevices. Thus, proximity to CCA is not explained by crevice use.

Crevice preference

In contrast to CCA, settlers showed a clear and consistent preference for crevices (**Figure 7 f, g, h** and Appendix **Table 6**). Across stones, the observed proportion of settlers located on crevices exceeded the expected proportion based on crevice area alone (Wilcoxon signed-rank test on per-stone deviations from expectation, $V = 91$, $p = 0.007$; one-sided test for preference). Despite the binomial mixed-effects model revealed variation in crevice use among stones (variance = 1.03, **Table 8**), the results still indicate that crevices represent a preferred settlement microhabitat independent of their areal availability.

DISCUSSION

This study provides a targeted examination of the ecological requirements underlying successful settlement in the temperate eastern Atlantic gorgonian species *Paramuricea* sp. Our experiments indicate for the first time in octocorals outside the tropics, that larval settlement is likely governed by a hierarchical process, in which both, biogenic habitat composition and microtopographic complexity jointly constrain natural recruitment. Specifically, the presence of particular CCA taxa and/or cues produced by the CCA holobiont, including the light-activated compound cycloprodigiosin (or similar molecules) synthesized by associated bacteria, may play a critical role in initiating settlement. Successful permanent attachment then seems depended on the availability of fine-scale microstructural features (e.g., crevices) within the surrounding substrate. This indicates that chemical induction alone is insufficient, and that physical habitat structure is an additional limiting factor.

This pattern mirrors processes, well documented in tropical scleractinian corals, highlighting a potentially conserved mechanism across coral functional groups despite their contrasting environments.

Species-specific CCA induction

The exclusive settlement of larvae on natural rocky substrates encrusted with crustose coralline algae (CCA), irrespective of substrate lithology, highlights the importance of biogenic surface properties for settlement success. The similar acceptance of sedimentary and volcanic substrates suggests that mineralogical characteristics play a subordinate role. The temporal stability of substrate preferences further indicates that these patterns are not strongly influenced by shifts in larval competence over time.

Paramuricea sp. settled on CCA-covered substrates originating from shallow (5 m) and deeper environments at comparable frequencies, despite differences in CCA species composition, all belonging to the family Lithophyllaceae. Members of this family are well known to induce larval settlement in a wide range of marine invertebrates, including tropical scleractinian corals (Tebben et al. 2015; Wahab et al. 2023), and have also been shown to enhance recruitment in Mediterranean gorgonians such as *Paramuricea clavata* (Zelli et al. 2020) and *Eunicella singularis* (Manea et al. 2025).

To date, only limited information is available on the chemical nature of settlement cues in octocorals, and experimentally validated inducers remain largely unidentified (but see (but see Manea et al. 2025, that suggests monosaccharids from bacteria could play a role). Even in scleractinian corals, where settlement has been more extensively studied, the biochemical compounds involved are unresolved for many taxa, highlighting a major knowledge gap in the chemical ecology of coral recruitment (Whitman et al. 2020). Together with the response to CYPRO our results support that attraction, and settlement is primarily driven by the recognition of specific chemical molecules associated with the CCA species and associated biofilms (Gómez-Lemos et al. 2018).

Chemical settlement induction

We demonstrated, for the first time, that CYPRO functions as a settlement cue for *Paramuricea* sp. larvae (Figure 7). However, follow-up experiments should be upscaled and investigate wider concentration ranges and detailed time dependency monitoring. Together with previous findings (Fiegel et al. 2025), this provides the first evidence suggesting that this chemically mediated settlement induction may operate across distinct cnidarian classes. Such a cross-class response suggests the possibility of a deeply conserved evolutionary mechanism underlying settlement cue

recognition, potentially involving homologous receptor systems or shared molecular pathways at the cellular level.

It remains unclear whether *Paramuricea* sp. larvae are naturally exposed to CYPRO, as its mechanism has been described as light-dependent (Petersen et al., 2021a, 2023), although activation can also occur under very low irradiance, with slower degradation kinetics. In the present study, experiments were conducted under minimal light conditions to approximate the natural environment while still allowing CYPRO activation. CYPRO is naturally produced by *Pseudoalteromonas rubra*, originally isolated from the CCA species *Hydrolithon reinboldii* collected in Guam, USA (Petersen et al., 2021b). Although this strain is of tropical origin, CYPRO-producing *Pseudoalteromonas* strains have also been reported from other regions, including the Mediterranean Sea (Gauthier 1976). Populations of *Paramuricea* along the Iberian margin inhabit mesophotic environments (Dias et al. 2020), where light, although reduced, remains present. In these habitats, coralline algae such as *Lithophyllum* and their associated microbial communities are common and are well adapted to very low light conditions (down to ~0.05% surface irradiance) (Ballesteros 2006). Notably, settlement experiments conducted in complete darkness resulted in only minimal larval settlement (Egger et al., unpublished data), suggesting that light may play an indirect or permissive role in settlement processes. Consequently, all experiments in this study were performed under low-light conditions designed to approximate the natural habitat. Further experimental work is required to disentangle the potential interaction between light availability and chemically mediated settlement cues, particularly with regard to CYPRO activation dynamics and larval sensory responses.

Dual effects of CCA and hierarchical control of settlement

Previous work has demonstrated that settlement cues provided by CCAs are highly species- and context-dependent (Harrington et al. 2004; Heyward & Negri 1999; Manea et al. 2025; Zelli et al. 2020). Consistent with this, only substrate with a subset of CCA species was selected by *Paramuricea* sp. as settlement substrate.

Our results might further suggest that the *Lithophyllaceae* species may also exert dual effects on temperate octocoral larvae as similar combinations of positive and negative cues have been described for tropical corals (Harrington et al. 2004; Jorissen et al. 2021; Wahab et al. 2023). These effects may include attractive signals that initiate settlement behaviour, while simultaneously discouraging direct attachment, for example through chemical deterrents or surface sloughing (Harrington et al. 2004). In line with this interpretation, larvae were observed accumulate on and swimming over the CCA during settlement trials, yet settlement was delayed by several days and rarely occurred directly on CCA, suggesting partial avoidance. Uptake of the settlement cue (CYPRO), visible as a colour change (Fiegel et al. 2025; Pomeroy et al. 2023), did not directly trigger

attachment at the point of contact. This suggests that larvae initially respond to biochemical cues but ultimately select suitable microhabitat features for permanent attachment, potentially avoiding direct competition with the algae. Such delays may allow larvae to evaluate physical and biological conditions before undergoing irreversible settlement. Extensive exploratory behaviour, including repeated short-term attachments, is well documented in tropical coral larvae (but has not been investigated in detail for non-tropical octocorals) and supports the concept of an active decision-making process prior to metamorphosis (Hadfield & Paul 2001; Pechenik 1999; Raimondi & Morse 2000).

Microhabitat selection

Spatial analyses revealed no uniform distribution pattern of recruits. Settlement patterns varied strongly among replicate stones provided as substrate, with weak to strong small-scale (1-3mm radius) clustering detected in only 40% of substrates. The rest showing spatial distributions of the recruits consistent with complete randomness. This heterogeneity suggests that recruits do not aggregate due to conspecific attraction but rather respond to fine-scale microhabitat differences. Small crevices, depressions, and surface irregularities provide favourable settlement sites and are known to be preferentially selected by tropical octocoral larvae (Martínez-Quintana et al. 2023). These microhabitats offer protection from hydrodynamic stress, predation, and sediment abrasion, while also facilitating the accumulation of organic particles (Doropoulos et al. 2016; Levenstein et al. 2022; Nozawa 2008; Whalan et al. 2015), which likely contributes to their attractiveness for settlement in both tropical and non-tropical gorgonians. However, such sheltered environments may also promote detritus buildup and reduced water flow, potentially limiting food delivery and self-cleaning processes, thereby creating a trade-off that can negatively affect post-settlement survival (Doropoulos et al. 2016; Egger et al. 2025; Randall et al. 2021).

Implications for recruitment and restoration

Successful settlement remains a major challenge for temperate and cold-water corals under aquarium conditions, despite being a prerequisite for experimental studies on early life ecology and other aspects of coral biology. In contrast to tropical corals, where a well-established aquarium trade enables the maintenance of corals at virtually all life stages, most non-tropical coral species cannot yet be reliably reared or settled in captivity (but see Egger et al. 2025 and; Giordano et al. 2026 that successfully settle and maintained temperate octocorals in captivity). A common limitation during larval rearing is the consistently low rate of settlement, or complete failure of larvae to settle (Linares et al. 2008; Rakka et al. 2021; Viladrich et al. 2022). Our results indicate that larval settlement induction in a circalittoral / mesophotic gorgonian does not require the cultivation of deep-water CCA species, as shallow-water CCA appeared to provide

functionally suitable settlement cues. Thus, for experimental applications requiring reliable larval settlement under aquarium conditions, artificial substrates designed to replicate the complex crevice and cavity microtopography found in natural habitats could be deliberately engineered, and either preconditioned in shallow water to promote colonization by appropriate biofilms and CCA communities or alternatively with the settlement cue CYPRO to enhance settlement success. Future studies should investigate which microstructural characteristics, such as size, shape, and surface complexity, as well optimizing beneficial CYPRO concentrations, most effectively promote settlement and early post-settlement survival for temperate octocoral larvae. Because our spatial analyses were based on two-dimensional data, incorporating three-dimensional microhabitat characterization would provide a more informative framework for modelling optimal settlement conditions.

Conclusion

Our results suggest that settlement in *Paramuricea* sp. may depend on the interaction between species-specific biochemical cues and fine-scale substrate structure, with chemical signals initiating settlement behaviour but not determining final attachment. However, key aspects of this process remain unresolved, including the mechanisms of cue perception, the identity and origin of the relevant compounds, and the role of associated microbial communities. It also remains unclear how environmental factors, such as light availability, modulate these interactions under natural conditions.

These uncertainties indicate that recruitment in temperate gorgonians is still only partially understood and may be highly sensitive to changes in both biogenic habitat composition and structural complexity. Our findings highlight that successful recruitment is closely linked to the availability of suitable microhabitat features at fine spatial scales. Consequently, habitat degradation that alters crustose coralline algal (CCA) communities or reduces microtopographic complexity may have disproportionate effects on recruitment success and long-term population persistence.

Addressing these knowledge gaps will be critical for improving predictions of population dynamics and for informing effective conservation and restoration strategies.

Acknowledgements

We are grateful for the technical assistance at the Ramalhete Marine Station that was kindly provided by João Reis and André Lopes. We further extend our sincere thanks to master Casimiro and his fishing crew for their invaluable collaboration and support in collecting the adult coral

652 specimens along the Sagres coast in southwestern Iberia. We are also grateful to Sheena Chung,
653 Chiara Favaretto and Manuela Quiroga for their immense support during the coral spawning season.

654 Funding

655 This study received Portuguese national funds from FCT - Foundation for Science and Technology
656 through contracts UID/04326/2025, UID/PRR/04326/2025 and LA/P/0101/2020
657 (DOI:10.54499/LA/P/0101/2020), Doctoral Scholarship SFRH/BD/151455/2021 to CE,
658 CEECINST/0014/2018 to AHE, as well as from funds from RESTORESEAS (2020–2021 Biodiversa+ and
659 Water JPI joint call for research projects under the Bio-divRestore ERA-NET Cofund (grant agreement
660 no. 101003777) and FCT (DivRestore/0013/2020); and CORALFORESTS (Fundação Belmiro de
661 Azevedo).

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APPENDIX

Table 1 Total settlement per substrate across the experimental period.

Shown are the total numbers of newly settled larvae per substrate and replicate (Rep 1–3), summed across the entire experimental period. Mean, standard deviation (SD), and standard error (SE) are calculated across replicates for each substrate. These values were used to assess overall substrate settlement preference independent of post-settlement mortality.

Substrate	Rep 1	Rep 2	Rep 3	Total settlement Mean	SD	SE
1	18	2	22	14	10.6	6.12
2	10	37	3	16.7	17.9	10.3
3	0	0	0	0	0	0
4	0	0	0	0	0	0
5	2	19	14	11.7	9.2	5.29
6	0	0	0	0	0	0

Table 2 Settlement probability for each substrate, calculated as the mean of a binary variable indicating the presence (1) or absence (0) of settlement per observation. Values represent the proportion of observations with at least one settler across all replicates and time points (n = 45 per substrate).

Substrate	Settlement probability (%)	n
1	26.7	45
2	28.9	45
3	0	45
4	0	45
5	28.9	45
6	0	45

Table 3 Results of a negative binomial generalized linear mixed model testing the effects of substrate and larval age on settlement intensity (number of newly settled larvae). Larval age was modelled using a natural spline (df = 2).

Model information	Predictor	Estimate	SE	z	p
Distribution: Negative binomial (log link) Observations: 135 Replicates: 3 AIC: 276.3	Intercept	-2.34	0.73	-3.21	0.001**
	Substrate 2	0.13	0.45	0.29	0.769
	Substrate 5	-0.22	0.46	-0.49	0.626
	Time (spline 1)	1.69	1.36	1.24	0.215
	Time (spline 2)	-10.29	2.07	-4.97	<0.001***

Table 4 Pairwise comparisons of settlement intensity among substrates supporting settlement (1, 2, and 5), based on estimated marginal means from a negative binomial GLMM. Estimates represent differences on the log scale, and p-values were adjusted for multiple comparisons using the Benjamini–Hochberg method.

Comparison	Estimate	p
1 vs 2	-0.131	0.77
1 vs 5	0.224	0.77
2 vs 5	0.356	0.77

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685 **Table 5** Raw data of Experiment 2

ID	replicate	duration	concentration	total larvae	swimming	attached	metamorphosis	settlement	dissolved
NEG-1-1 day	1	1 day	NEG	3	3	0	0	0	0
NEG-2-1 day	2	1 day	NEG	3	3	0	0	0	0
NEG-3-1 day	3	1 day	NEG	3	3	0	0	0	0
POSI-1-1 day	1	1 day	POSI	3	3	0	0	0	0
POSI-2-1 day	2	1 day	POSI	3	3	0	0	0	0
POSI-3-1 day	3	1 day	POSI	3	3	0	0	0	0
POSII-1-1 day	1	1 day	POSII	3	3	0	0	0	0
POSII-2-1 day	2	1 day	POSII	3	3	0	0	0	0
POSII-3-1 day	3	1 day	POSII	3	3	0	0	0	0
0.05-1-1 day	1	1 day	0.05	3	3	0	0	0	0
0.05-2-1 day	2	1 day	0.05	3	3	0	0	0	0
0.05-3-1 day	3	1 day	0.05	3	3	0	0	0	0
0.13-1-1 day	1	1 day	0.13	3	3	0	0	0	0
0.13-2-1 day	2	1 day	0.13	3	3	0	0	0	0
0.13-3-1 day	3	1 day	0.13	3	3	0	0	0	0
0.26-1-1 day	1	1 day	0.26	4	4	0	0	0	0
0.26-2-1 day	2	1 day	0.26	3	3	0	0	0	0
0.26-3-1 day	3	1 day	0.26	3	3	0	0	0	0
0.39-1-1 day	1	1 day	0.39	3	3	0	0	0	0
0.39-2-1 day	2	1 day	0.39	3	3	0	0	0	0
0.39-3-1 day	3	1 day	0.39	3	3	0	0	0	0
0.53-1-1 day	1	1 day	0.53	3	2	0	0	0	1
0.53-2-1 day	2	1 day	0.53	3	3	0	0	0	0
0.53-3-1 day	3	1 day	0.53	3	3	0	0	0	0
NEG-1-2 days	1	2 days	NEG	3	3	0	0	0	0
NEG-2-2 days	2	2 days	NEG	3	3	0	0	0	0
NEG-3-2 days	3	2 days	NEG	3	3	0	0	0	0
POSI-1-2 days	1	2 days	POSI	3	3	0	0	0	0
POSI-2-2 days	2	2 days	POSI	3	3	0	0	0	0
POSI-3-2 days	3	2 days	POSI	3	3	0	0	0	0
POSII-1-2 days	1	2 days	POSII	3	3	0	0	0	0
POSII-2-2 days	2	2 days	POSII	3	3	0	0	0	0
POSII-3-2 days	3	2 days	POSII	3	3	0	0	0	0
0.05-1-2 days	1	2 days	0.05	3	3	0	0	0	0
0.05-2-2 days	2	2 days	0.05	3	3	0	0	0	0
0.05-3-2 days	3	2 days	0.05	3	3	0	0	0	0
0.13-1-2 days	1	2 days	0.13	3	3	0	0	0	0
0.13-2-2 days	2	2 days	0.13	3	3	0	0	0	0
0.13-3-2 days	3	2 days	0.13	3	3	0	0	0	0
0.26-1-2 days	1	2 days	0.26	4	4	0	0	0	0
0.26-2-2 days	2	2 days	0.26	3	3	0	0	0	0
0.26-3-2 days	3	2 days	0.26	3	3	0	0	0	0
0.39-1-2 days	1	2 days	0.39	3	1	2	0	0	0
0.39-2-2 days	2	2 days	0.39	3	2	1	0	0	0
0.39-3-2 days	3	2 days	0.39	3	2	1	0	0	0
0.53-1-2 days	1	2 days	0.53	3	1	0	0	1	1
0.53-2-2 days	2	2 days	0.53	3	1	2	0	0	0
0.53-3-2 days	3	2 days	0.53	3	1	0	0	2	0

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NEG-1-5 days	1	5 days	NEG	3	3	0	0	0	0
NEG-2-5 days	2	5 days	NEG	3	3	0	0	0	0
NEG-3-5 days	3	5 days	NEG	3	3	0	0	0	0
POSI-1-5 days	1	5 days	POSI	3	3	0	0	0	0
POSI-2-5 days	2	5 days	POSI	3	3	0	0	0	0
POSI-3-5 days	3	5 days	POSI	3	3	0	0	0	0
POSII-1-5 days	1	5 days	POSII	3	3	0	0	0	0
POSII-2-5 days	2	5 days	POSII	3	3	0	0	0	0
POSII-3-5 days	3	5 days	POSII	3	3	0	0	0	0
0.05-1-5 days	1	5 days	0.05	3	3	0	0	0	0
0.05-2-5 days	2	5 days	0.05	3	3	0	0	0	0
0.05-3-5 days	3	5 days	0.05	3	3	0	0	0	0
0.13-1-5 days	1	5 days	0.13	3	3	0	0	0	0
0.13-2-5 days	2	5 days	0.13	3	3	0	0	0	0
0.13-3-5 days	3	5 days	0.13	3	3	0	0	0	0
0.26-1-5 days	1	5 days	0.26	4	2	0	0	2	0
0.26-2-5 days	2	5 days	0.26	3	3	0	0	0	0
0.26-3-5 days	3	5 days	0.26	3	3	0	0	0	0
0.39-1-5 days	1	5 days	0.39	3	1	0	0	0	2
0.39-2-5 days	2	5 days	0.39	3	2	0	0	0	1
0.39-3-5 days	3	5 days	0.39	3	2	0	0	1	0
0.53-1-5 days	1	5 days	0.53	3	1	0	0	0	2
0.53-2-5 days	2	5 days	0.53	3	1	0	0	2	0
0.53-3-5 days	3	5 days	0.53	3	1	0	0	2	0
NEG-1-9 days	1	9 days	NEG	3	3	0	0	0	0
NEG-2-9 days	2	9 days	NEG	3	3	0	0	0	0
NEG-3-9 days	3	9 days	NEG	3	3	0	0	0	0
POSI-1-9 days	1	9 days	POSI	3	3	0	0	0	0
POSI-2-9 days	2	9 days	POSI	3	3	0	0	0	0
POSI-3-9 days	3	9 days	POSI	3	3	0	0	0	0
POSII-1-9 days	1	9 days	POSII	3	3	0	0	0	0
POSII-2-9 days	2	9 days	POSII	3	3	0	0	0	0
POSII-3-9 days	3	9 days	POSII	3	3	0	0	0	0
0.05-1-9 days	1	9 days	0.05	3	3	0	0	0	0
0.05-2-9 days	2	9 days	0.05	3	3	0	0	0	0
0.05-3-9 days	3	9 days	0.05	3	3	0	0	0	0
0.13-1-9 days	1	9 days	0.13	3	3	0	0	0	0
0.13-2-9 days	2	9 days	0.13	3	3	0	0	0	0
0.13-3-9 days	3	9 days	0.13	3	3	0	0	0	0
0.26-1-9 days	1	9 days	0.26	4	2	0	0	2	0
0.26-2-9 days	2	9 days	0.26	3	3	0	0	0	0
0.26-3-9 days	3	9 days	0.26	3	1	0	0	2	0
0.39-1-9 days	1	9 days	0.39	3	0	1	0	0	2
0.39-2-9 days	2	9 days	0.39	3	1	0	0	0	2
0.39-3-9 days	3	9 days	0.39	3	1	0	0	0	2
0.53-1-9 days	1	9 days	0.53	3	1	0	0	0	2
0.53-2-9 days	2	9 days	0.53	3	1	0	0	2	0
0.53-3-9 days	3	9 days	0.53	3	1	0	0	2	0

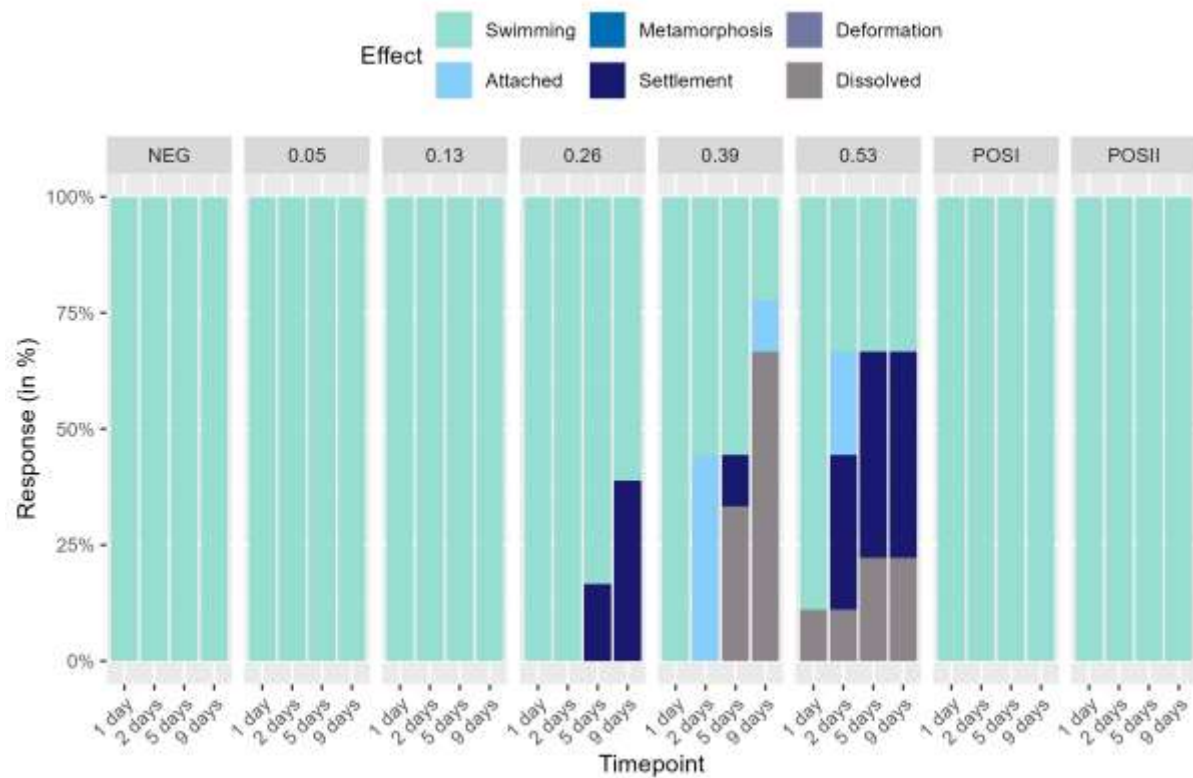


Figure 8 All effects of *Paramuricea* sp. larvae exposed to CYPRO observed in Exp.2

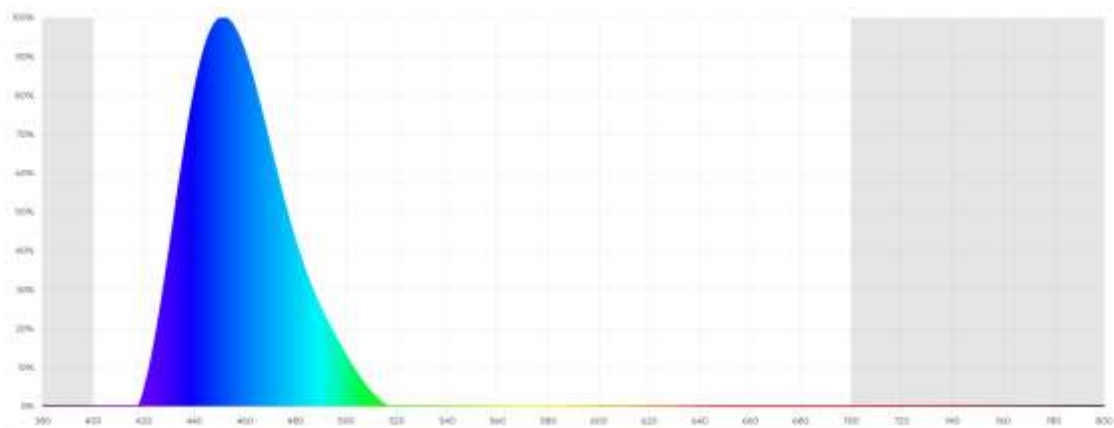
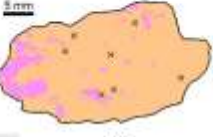
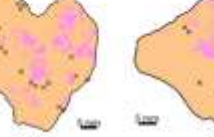
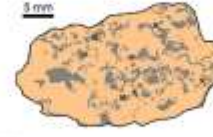
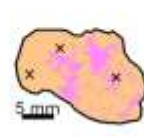
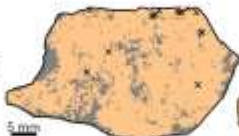
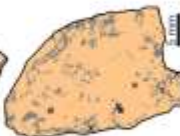
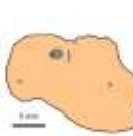
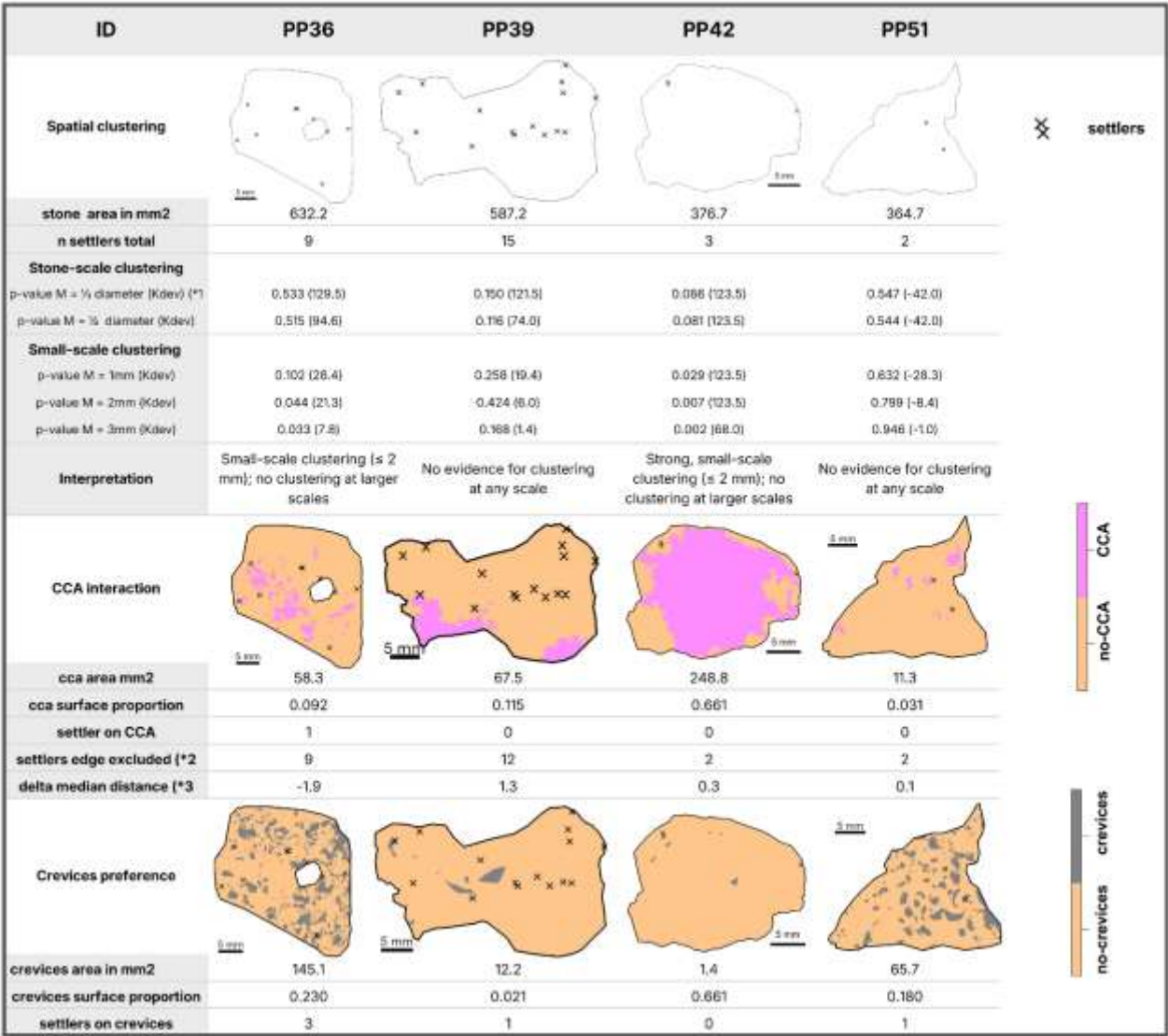


Figure 9 Light spectrum that was applied in Experiment 2. For illumination an Ecotech Marine Radion XR30 was used. The peak wavelength is at 451 nm, and the light intensity is 16 lux and 2 PAR. This was measured using a ICT PARwise device.

Table 6 Spatial settlement preferences of purple *Paramuricea* sp. larvae on natural substrates with different cover of crustose coralline algae (CCA) and crevices. (*1 Clustering strength was quantified at stone-scale (¼ and ½ of the minimum stone diameter) and at biologically relevant small spatial scales (1–3 mm). **M**= upper integration limit (in mm) defining the spatial scale over which clustering strength was calculated. **Kdev** is the clustering strength, calculated as the integrated deviation of the border-corrected Ripley's K-function from the expectation under complete spatial randomness (CSR). Positive values indicate clustering, negative values indicate inhibition, and values near zero indicate CSR-like patterns. Monte-Carlo **p-values** are the probability of observing a clustering strength at least as extreme as the observed value under CSR, estimated from 999 Monte-Carlo simulations within the empirical stone outlines. Lower p-values indicate stronger evidence for departure from CSR. (*2 remaining settlers after exclusion of settlers closer than 1mm to the edges (*3 Delta of computed median distance of settlers to next CCA area and medium random distance to CCA. Negative values indicate closer than random.

ID	PP01	PP03	PP10	PP22	PP24
Spatial clustering					
stone area in mm2	477.9	601.3	820.3	1067.5	977.4
n settlers total	7	13	18	17	15
Stone-scale clustering					
p-value M = ¼ diameter (Kdev) (*1)	0.858 (-38.3)	0.006 (267.2)	0.874 (-37.8)	0.361 (255.0)	0.344 (-263.8)
p-value M = ½ diameter (Kdev)	0.951 (8.6)	0.005 (176.6)	0.875 (-20.0)	0.114 (196.0)	0.138 (-197.1)
Small-scale clustering					
p-value M = 1mm (Kdev)	0.983 (-1.0)	0.151 (1.8)	0.790 (-1.0)	0.074 (28.1)	0.293 (22.5)
p-value M = 2mm (Kdev)	0.825 (-8.4)	0.08 (11.9)	0.901 (-0.9)	0.776 (2.9)	0.919 (1.4)
p-value M = 3mm (Kdev)	0.957 (-2.5)	0.027 (46.0)	0.592 (-9.0)	0.887 (-1.0)	0.915 (-1.0)
Interpretation:	No evidence for clustering at any scale	Strong stone-scale clustering; weak clustering at ~3 mm	No evidence for clustering at any scale	No clustering detected; weak, non-significant tendency at ~3 mm	No evidence for clustering at any scale
CCA interaction					
cca area mm2	49.0	114.7	102.3	131.2	48.5
cca surface proportion	0.103	0.191	0.125	0.123	0.050
settler on CCA	0	0	0	0	0
settlers edge excluded (*2)	7	13	17	15	11
delta median distance (*3)	-0.3	-1.2	-0.8	0.0	-1.8
Crevices preference					
crevices area in mm2	109.2	179.5	199.9	214.3	106.4
crevices surface proportion	0.228	0.298	0.244	0.201	0.109
settlers on crevices	6	11	13	10	7

ID	PP28	PP31	PP33	PP34	PP35
Spatial clustering					
stone area in mm ²	820.8	385.7	984.8	217.8	1412.6
n settlers total	13	7	12	3	3
Stone-scale clustering					
p-value M = 5 diameter (Kdev) [*1]	0.095 (-207.5)	0.692 (34.7)	0.491 (-154.7)	0.503 (-38.4)	0.596 (-548.9)
p-value M = 15 diameter (Kdev)	0.086 (-192.6)	0.717 (134.7)	0.550 (-65.1)	0.623 (-27.2)	0.560 (-513.8)
Small-scale clustering					
p-value M = 1mm (Kdev)	0.000 (16.8)	0.638 (18.7)	0.502 (-20.2)	0.816 (-28.2)	0.956 (-28.1)
p-value M = 2mm (Kdev)	0.039 (17.0)	0.060 (20.5)	0.678 (-8.2)	0.875 (-8.4)	0.990 (-8.2)
p-value M = 3mm (Kdev)	0.909 (-2.7)	0.050 (5.8)	0.952 (-1.0)	0.988 (-1.0)	0.998 (-1.0)
Interpretation	Strong, small-scale clustering (≤ 2 mm); no clustering at larger scales	Strong stone-scale clustering; weak clustering at ~3 mm	No evidence for clustering at any scale	No evidence for clustering at any scale	No evidence for clustering at any scale
CCA interaction					
cca area mm ²	294.4	64.1	99.6	44.0	131.8
cca surface proportion	0.359	0.166	0.101	0.202	0.093
settler on CCA	1	0	0	0	0
settlers edge excluded (*2)	8	5	12	2	3
delta median distance [*3]	0.3	-0.1	-1.2	-0.1	-1.1
Crevices preference					
crevices area in mm ²	135.2	56.4	168.6	3.4	453.5
crevices surface proportion	0.165	0.146	0.171	0.016	0.321
settlers on crevices	3	4	8	1	1



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715 **Table 7** CCA/Crevice use dependence: Linear Mixed-effects model testing the effect of crevice presence on distance to CCA
716 [lmer(dist_to_cca ~ on_crevice + (1 | stone_id)).

Predictor	Estimate	Std. Error	t value	Random effects:		
				Effect	Variance	Std. Dev.
Intercept	2.615	0.746	3.505	Stone ID	5.446	2.334
Crevice (TRUE)	-0.689	0.588	-1.172	Residual	9.331	3.055

Variation explained by stone: $5.446 / (5.446 + 9.331) \approx 0.37$

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719 **Table 8** Effect of stone identity: General linear mixed-effects model of crevice use [glmer(on_crevice ~ (1 | stone_id))].

Effect	Variance	Std. Dev.	Estimate	Std. Error	z value	p value
Stone ID	1.03	1.015	-0.148	0.347	-0.425	0.671

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723 SUPPLEMENT

724 **Table 9** Daily counts of larval attachment, total settlers, new settlers, and settler mortality per substrate, with replicate-level
725 values and summary statistics. Replicate-level values (R1–R3) are shown alongside mean, standard deviation (SD), and
726 standard error (SE) calculated across replicates for each substrate and day post-experiment start.

Date	Substrate	Days post experiment. start	Larvae attached						Settlers total						New settlers			Settlers died		
			R1	R2	R3	Mean	SD	SE	R1	R2	R3	Mean	SD	SE	R1	R2	R3	R1	R2	R3
11 September 2024	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
11 September 2024	2	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
11 September 2024	3	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
11 September 2024	4	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
11 September 2024	5	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
11 September 2024	6	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
12 September 2024	1	2	1	1	7	3	3.5	2	0	0	0	0	0	0	0	0	0	0	0	0
12 September 2024	2	2	2	17	0	6.3	9.3	5.4	0	0	0	0	0	0	0	0	0	0	0	0
12 September 2024	3	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
12 September 2024	4	2	1	1	5	2.3	2.3	1.3	0	0	0	0	0	0	0	0	0	0	0	0
12 September 2024	5	2	0	9	1	3.3	4.9	2.8	0	0	0	0	0	0	0	0	0	0	0	0
12 September 2024	6	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
13 September 2024	1	3	0	0	3	1	1.7	1	0	0	9	3	5.2	3	0	0	9	0	0	0
13 September 2024	2	3	1	13	0	4.7	7.2	4.2	1	1	0	0.7	0.6	0.3	1	1	0	0	0	0
13 September 2024	3	3	1	0	0	0.3	0.6	0.3	0	0	0	0	0	0	0	0	0	0	0	0
13 September 2024	4	3	0	2	3	1.7	1.5	0.9	0	0	0	0	0	0	0	0	0	0	0	0
13 September 2024	5	3	3	2	0	1.7	1.5	0.9	0	5	0	1.7	2.9	1.7	0	5	0	0	0	0
13 September 2024	6	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
14 September 2024	1	4	2	0	2	1.3	1.2	0.7	7	0	17	8	8.5	4.9	7	0	8	0	0	0
14 September 2024	2	4	0	1	0	0.3	0.6	0.3	2	12	0	4.7	6.4	3.7	1	11	0	0	0	0
14 September 2024	3	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
14 September 2024	4	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
14 September 2024	5	4	0	0	3	1	1.7	1	1	6	3	3.3	2.5	1.5	1	1	3	0	0	0
14 September 2024	6	4	0	0	1	0.3	0.6	0.3	0	0	0	0	0	0	0	0	0	0	0	0
15 September 2024	1	5	1	0	1	0.7	0.6	0.3	7	0	19	8.7	9.6	5.5	0	0	2	0	0	0
15 September 2024	2	5	0	2	0	0.7	1.2	0.7	7	16	3	8.7	6.7	3.8	0	5	3	0	-1	0
15 September 2024	3	5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
15 September 2024	4	5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
15 September 2024	5	5	1	2	1	1.3	0.6	0.3	1	12	5	6	5.6	3.2	0	6	2	0	0	0
15 September 2024	6	5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
16 September 2024	1	6	1	0	2	1	1	0.6	13	0	19	10.7	9.7	5.6	4	0	0	0	0	0
16 September 2024	2	6	1	0	0	0.3	0.6	0.3	5	11	2	6	4.6	2.6	0	0	0	-2	0	-1
16 September 2024	3	6	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
16 September 2024	4	6	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
16 September 2024	5	6	0	0	0	0	0	0	1	10	9	6.7	4.9	2.8	0	0	4	0	-2	0
16 September 2024	6	6	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
17 September 2024	1	7	0	0	0	0	0	0	16	1	21	12.7	10.4	6	3	1	2	0	0	0
17 September 2024	2	7	1	0	0	0.3	0.6	0.3	5	24	5	11.3	11	6.3	2	13	0	-2	0	0
17 September 2024	3	7	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
17 September 2024	4	7	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
17 September 2024	5	7	0	1	3	1.3	1.5	0.9	1	13	12	8.7	6.7	3.8	0	4	3	0	-1	0
17 September 2024	6	7	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
18 September 2024	1	8	1	0	0	0.3	0.6	0.3	17	1	22	13.3	11	6.3	1	0	1	0	0	0
18 September 2024	2	8	1	2	0	1	1	0.6	7	27	5	13	12.2	7	2	3	0	0	0	0
18 September 2024	3	8	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
18 September 2024	4	8	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
18 September 2024	5	8	0	0	0	0	0	0	1	16	13	10	7.9	4.6	0	3	1	0	0	0
18 September 2024	6	8	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
19 September 2024	1	9	0	0	0	0	0	0	20	2	22	14.7	11	6.4	3	1	0	0	0	-1
19 September 2024	2	9	0	0	1	0.3	0.6	0.3	10	31	5	15.3	13.8	8	3	4	0	0	0	0
19 September 2024	3	9	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
19 September 2024	4	9	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
19 September 2024	5	9	0	0	0	0	0	0	1	16	13	10	7.9	4.6	0	0	0	0	0	0
19 September 2024	6	9	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
20 September 2024	1	10	0	0	0	0	0	0	20	2	21	14.3	10.7	6.2	0	0	0	0	0	-1
20 September 2024	2	10	0	0	0	0	0	0	10	31	4	15	14.2	8.2	0	0	0	0	0	-1
20 September 2024	3	10	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
20 September 2024	4	10	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
20 September 2024	5	10	0	0	0	0	0	0	1	16	14	10.3	8.1	4.7	0	0	1	0	0	0
20 September 2024	6	10	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

(cont.)

Date	Substrate	Days post experiment. start	Larvae attached						Settlers total						New settlers			Settlers died		
			R1	R2	R3	Mean	SD	SE	R1	R2	R3	Mean	SD	SE	R1	R2	R3	R1	R2	R3
21 September 2024	1	11	0	0	0	0	0	0	19	2	19	13.3	9.8	5.7	0	0	0	-1	0	-2
21 September 2024	2	11	0	0	0	0	0	0	11	31	3	15	14.4	8.3	1	0	0	0	0	-1
21 September 2024	3	11	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
21 September 2024	4	11	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
21 September 2024	5	11	0	0	0	0	0	0	1	12	14	9	7	4	1	0	0	0	-5	0
21 September 2024	6	11	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
22 September 2024	1	12	0	0	0	0	0	0	18	1	19	12.7	10.1	5.8	0	0	0	-1	-1	0
22 September 2024	2	12	0	0	0	0	0	0	11	29	3	14.3	13.3	7.7	0	0	0	0	-2	0
22 September 2024	3	12	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
22 September 2024	4	12	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
22 September 2024	5	12	0	0	0	0	0	0	1	12	14	9	7	4	0	0	0	0	0	0
22 September 2024	6	12	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
23 September 2024	1	13	0	0	0	0	0	0	15	1	19	11.7	9.5	5.5	0	0	0	-3	0	0
23 September 2024	2	13	0	0	0	0	0	0	10	25	3	12.7	11.2	6.5	0	0	0	-1	-4	0
23 September 2024	3	13	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
23 September 2024	4	13	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
23 September 2024	5	13	0	0	0	0	0	0	1	9	14	8	6.6	3.8	0	0	0	0	-3	0
23 September 2024	6	13	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
24 September 2024	1	14	0	0	0	0	0	0	15	0	17	10.7	9.3	5.4	0	0	0	0	-1	-2
24 September 2024	2	14	0	0	0	0	0	0	14	20	3	12.3	8.6	5	0	0	0	0	-5	0
24 September 2024	3	14	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
24 September 2024	4	14	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
24 September 2024	5	14	0	0	0	0	0	0	1	9	13	7.7	6.1	3.5	0	0	0	0	0	-1
24 September 2024	6	14	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
25 September 2024	1	15	0	0	0	0	0	0	20	0	4	8	10.6	6.1	0	0	0	0	0	0
25 September 2024	2	15	0	0	0	0	0	0	11	19	3	11	8	4.6	0	0	0	-3	-1	0
25 September 2024	3	15	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
25 September 2024	4	15	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
25 September 2024	5	15	0	0	0	0	0	0	1	9	13	7.7	6.1	3.5	0	0	0	0	0	0
25 September 2024	6	15	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

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recruit_id	recruit	stone_id	x position	y position	on_cca	on_crevice	dist_to_cca	stone_area	cca_prop	cre_prop	cre_in_cca_prop	cre_out_cca_prop
PP35_1	1	PP35	4.1826	21.64	FALSE	FALSE	1.446	1427.3	0.0900	0.1938	0.005657	0.1882
PP35_2	2	PP35	21.104	45.88	FALSE	FALSE	2.054	1427.3	0.0900	0.1938	0.005657	0.1882
PP35_3	3	PP35	4.1621	9.536	FALSE	FALSE	10.385	1427.3	0.0900	0.1938	0.005657	0.1882
PP42_1	1	PP42	24.937	12.41	FALSE	FALSE	0.507	376.7	0.7183	0.0037	0.002476	0.0012
PP42_2	2	PP42	5.108	16.94	FALSE	FALSE	0.783	376.7	0.7183	0.0037	0.002476	0.0012
PP42_3	3	PP42	5.217	16.5	FALSE	FALSE	0.826	376.7	0.7183	0.0037	0.002476	0.0012
PP22_1	1	PP22	10.828	24.7	FALSE	TRUE	0.898	1067.5	0.1229	0.2008	0.000647	0.2001
PP22_2	2	PP22	16.767	17.53	FALSE	FALSE	1.941	1067.5	0.1229	0.2008	0.000647	0.2001
PP22_3	3	PP22	19.676	14.22	FALSE	TRUE	0.240	1067.5	0.1229	0.2008	0.000647	0.2001
PP22_4	4	PP22	20.973	13.28	FALSE	TRUE	0.699	1067.5	0.1229	0.2008	0.000647	0.2001
PP22_5	5	PP22	23.345	12.88	FALSE	TRUE	0.588	1067.5	0.1229	0.2008	0.000647	0.2001
PP22_6	6	PP22	32.875	16.19	FALSE	TRUE	0.613	1067.5	0.1229	0.2008	0.000647	0.2001
PP22_7	7	PP22	31.622	21.91	FALSE	TRUE	0.746	1067.5	0.1229	0.2008	0.000647	0.2001
PP22_8	8	PP22	10.101	30.28	FALSE	TRUE	2.417	1067.5	0.1229	0.2008	0.000647	0.2001
PP22_9	9	PP22	27.908	7.058	FALSE	FALSE	0.500	1067.5	0.1229	0.2008	0.000647	0.2001
PP22_10	10	PP22	9.43	27.15	FALSE	FALSE	0.848	1067.5	0.1229	0.2008	0.000647	0.2001
PP22_11	11	PP22	12.114	23.21	FALSE	TRUE	1.185	1067.5	0.1229	0.2008	0.000647	0.2001
PP22_12	12	PP22	29.116	6.208	FALSE	FALSE	0.493	1067.5	0.1229	0.2008	0.000647	0.2001
PP22_13	13	PP22	36.365	15.25	FALSE	FALSE	2.426	1067.5	0.1229	0.2008	0.000647	0.2001
PP22_14	14	PP22	24.911	14.04	FALSE	TRUE	0.747	1067.5	0.1229	0.2008	0.000647	0.2001
PP22_15	15	PP22	15.872	37.48	FALSE	FALSE	6.955	1067.5	0.1229	0.2008	0.000647	0.2001
PP22_16	16	PP22	16.588	36.01	FALSE	TRUE	5.600	1067.5	0.1229	0.2008	0.000647	0.2001
PP22_17	17	PP22	17.528	37.04	FALSE	FALSE	6.847	1067.5	0.1229	0.2008	0.000647	0.2001
PP39_1	1	PP39	30.257	19.92	FALSE	FALSE	14.073	587.2	0.1150	0.0208	0.000127	0.0207
PP39_2	2	PP39	30.485	18.05	FALSE	FALSE	13.512	587.2	0.1150	0.0208	0.000127	0.0207
PP39_3	3	PP39	30.762	11.52	FALSE	FALSE	7.035	587.2	0.1150	0.0208	0.000127	0.0207
PP39_4	4	PP39	29.495	11.67	FALSE	FALSE	7.324	587.2	0.1150	0.0208	0.000127	0.0207
PP39_5	5	PP39	27.396	11.08	FALSE	FALSE	7.155	587.2	0.1150	0.0208	0.000127	0.0207
PP39_6	6	PP39	25.415	12.51	FALSE	FALSE	7.422	587.2	0.1150	0.0208	0.000127	0.0207
PP39_7	7	PP39	22.01	11.55	FALSE	FALSE	3.902	587.2	0.1150	0.0208	0.000127	0.0207
PP39_8	8	PP39	15.277	9.138	FALSE	FALSE	1.069	587.2	0.1150	0.0208	0.000127	0.0207
PP39_9	9	PP39	5.97	11.52	FALSE	FALSE	0.250	587.2	0.1150	0.0208	0.000127	0.0207
PP39_10	10	PP39	35.91	17.22	FALSE	FALSE	12.945	587.2	0.1150	0.0208	0.000127	0.0207
PP39_11	11	PP39	22.366	11.04	FALSE	FALSE	4.076	587.2	0.1150	0.0208	0.000127	0.0207
PP39_12	12	PP39	30.881	22.68	FALSE	FALSE	15.827	587.2	0.1150	0.0208	0.000127	0.0207
PP39_13	13	PP39	16.544	15.12	FALSE	FALSE	0.508	587.2	0.1150	0.0208	0.000127	0.0207
PP39_14	14	PP39	3.079	18.17	FALSE	TRUE	7.069	587.2	0.1150	0.0208	0.000127	0.0207
PP39_15	15	PP39	7	19.59	FALSE	FALSE	8.104	587.2	0.1150	0.0208	0.000127	0.0207
PP34_1	1	PP34	2.35	7.705	FALSE	FALSE	2.805	217.8	0.2021	0.0157	0.000408	0.0153
PP34_2	2	PP34	7.097	11.82	FALSE	TRUE	0.467	217.8	0.2021	0.0157	0.000408	0.0153
PP34_3	3	PP34	15.968	7.224	FALSE	FALSE	0.097	217.8	0.2021	0.0157	0.000408	0.0153
PP36_1	1	PP36	27.632	17.11	FALSE	FALSE	2.131	651.8	0.0894	0.2227	0.000335	0.2224
PP36_2	2	PP36	19.655	19.43	FALSE	FALSE	3.559	651.8	0.0894	0.2227	0.000335	0.2224
PP36_3	3	PP36	22.851	16.46	FALSE	TRUE	2.295	651.8	0.0894	0.2227	0.000335	0.2224
PP36_4	4	PP36	15.858	21.69	FALSE	FALSE	1.156	651.8	0.0894	0.2227	0.000335	0.2224
PP36_5	5	PP36	15.407	21.72	FALSE	FALSE	1.289	651.8	0.0894	0.2227	0.000335	0.2224
PP36_6	6	PP36	1.949	14.43	TRUE	FALSE	0.000	651.8	0.0894	0.2227	0.000335	0.2224
PP36_7	7	PP36	21.61	4.355	FALSE	TRUE	1.783	651.8	0.0894	0.2227	0.000335	0.2224
PP36_8	8	PP36	6.422	15.78	FALSE	FALSE	0.610	651.8	0.0894	0.2227	0.000335	0.2224
PP36_9	9	PP36	4.467	22.66	FALSE	TRUE	0.284	651.8	0.0894	0.2227	0.000335	0.2224
PP31_1	1	PP31	4.246	20.63	FALSE	TRUE	0.634	385.7	0.1662	0.1462	0.011291	0.1349
PP31_2	2	PP31	1.562	14.38	FALSE	TRUE	1.191	385.7	0.1662	0.1462	0.011291	0.1349
PP31_3	3	PP31	4.276	9.895	FALSE	TRUE	0.645	385.7	0.1662	0.1462	0.011291	0.1349
PP31_4	4	PP31	4.879	10.23	FALSE	TRUE	0.344	385.7	0.1662	0.1462	0.011291	0.1349
PP31_5	5	PP31	8.195	7.751	FALSE	FALSE	0.343	385.7	0.1662	0.1462	0.011291	0.1349
PP31_6	6	PP31	7.425	3.53	FALSE	FALSE	0.548	385.7	0.1662	0.1462	0.011291	0.1349
PP31_7	7	PP31	9.937	1.286	FALSE	FALSE	0.758	385.7	0.1662	0.1462	0.011291	0.1349

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recruit_id	recruit	stone_id	x position	y position	on_cca	on_crevice	dist_to_cca	stone_area	cca_prop	cre_prop	cre_in_cca_prop	cre_out_cca_prop
PP51_1	1	PP51	18.832	13.13	FALSE	FALSE	0.458	364.7	0.0309	0.1803	0.001660	0.1786
PP51_2	2	PP51	22.076	8.213	FALSE	TRUE	1.633	364.7	0.0309	0.1803	0.001660	0.1786
PP35_1	1	PP35	4.1826	21.64	FALSE	FALSE	0.242	1427.3	0.0944	0.3075	0.011304	0.2962
PP35_2	2	PP35	21.104	45.88	FALSE	TRUE	0.642	1427.3	0.0944	0.3075	0.011304	0.2962
PP35_3	3	PP35	4.1621	9.536	FALSE	FALSE	0.528	1427.3	0.0944	0.3075	0.011304	0.2962
PP28_1	1	PP28	34.163	24.8	FALSE	FALSE	1.209	820.6	0.3587	0.1647	0.020346	0.1444
PP28_2	2	PP28	36.87	24.74	FALSE	FALSE	2.056	820.6	0.3587	0.1647	0.020346	0.1444
PP28_3	3	PP28	28.454	24.07	FALSE	TRUE	0.595	820.6	0.3587	0.1647	0.020346	0.1444
PP28_4	4	PP28	37.956	20.85	FALSE	TRUE	0.660	820.6	0.3587	0.1647	0.020346	0.1444
PP28_5	5	PP28	37.187	10.76	FALSE	TRUE	0.203	820.6	0.3587	0.1647	0.020346	0.1444
PP28_6	6	PP28	15.694	13.25	FALSE	FALSE	1.096	820.6	0.3587	0.1647	0.020346	0.1444
PP28_7	7	PP28	16.373	25.24	FALSE	FALSE	0.489	820.6	0.3587	0.1647	0.020346	0.1444
PP28_8	8	PP28	33.567	24.74	FALSE	FALSE	1.073	820.6	0.3587	0.1647	0.020346	0.1444
PP28_9	9	PP28	35.106	25.51	FALSE	FALSE	1.932	820.6	0.3587	0.1647	0.020346	0.1444
PP28_10	10	PP28	29.676	25.06	FALSE	FALSE	1.266	820.6	0.3587	0.1647	0.020346	0.1444
PP28_11	11	PP28	33.25	25.15	FALSE	FALSE	1.520	820.6	0.3587	0.1647	0.020346	0.1444
PP28_12	12	PP28	28.906	24.34	FALSE	FALSE	0.575	820.6	0.3587	0.1647	0.020346	0.1444
PP28_13	13	PP28	19.902	17.1	TRUE	FALSE	0.000	820.6	0.3587	0.1647	0.020346	0.1444
PP24_1	1	PP24	35.911	18.97	FALSE	FALSE	10.407	977.4	0.0497	0.1088	0.000852	0.1080
PP24_2	2	PP24	36.79	20.39	FALSE	TRUE	11.170	977.4	0.0497	0.1088	0.000852	0.1080
PP24_3	3	PP24	28.218	21.08	FALSE	FALSE	2.582	977.4	0.0497	0.1088	0.000852	0.1080
PP24_4	4	PP24	14.721	25.76	FALSE	TRUE	1.846	977.4	0.0497	0.1088	0.000852	0.1080
PP24_5	5	PP24	13.637	27.04	FALSE	TRUE	0.553	977.4	0.0497	0.1088	0.000852	0.1080
PP24_6	6	PP24	22.504	9.253	FALSE	FALSE	9.117	977.4	0.0497	0.1088	0.000852	0.1080
PP24_7	7	PP24	36.987	8.465	FALSE	TRUE	16.449	977.4	0.0497	0.1088	0.000852	0.1080
PP24_8	8	PP24	38.76	14.77	FALSE	FALSE	14.313	977.4	0.0497	0.1088	0.000852	0.1080
PP24_9	9	PP24	17.677	12.01	FALSE	TRUE	7.060	977.4	0.0497	0.1088	0.000852	0.1080
PP24_10	10	PP24	39.204	10.93	FALSE	TRUE	16.553	977.4	0.0497	0.1088	0.000852	0.1080
PP24_11	11	PP24	26.445	32.01	FALSE	FALSE	0.040	977.4	0.0497	0.1088	0.000852	0.1080
PP24_12	12	PP24	32.849	30.78	FALSE	FALSE	2.371	977.4	0.0497	0.1088	0.000852	0.1080
PP24_13	13	PP24	4.1076	17.04	FALSE	FALSE	15.835	977.4	0.0497	0.1088	0.000852	0.1080
PP24_14	14	PP24	40.435	15.41	FALSE	FALSE	15.650	977.4	0.0497	0.1088	0.000852	0.1080
PP24_15	15	PP24	27.332	30.29	FALSE	TRUE	0.051	977.4	0.0497	0.1088	0.000852	0.1080
PP10_1	1	PP10	6.801	27.02	FALSE	TRUE	0.334	820.3	0.1247	0.2437	0.007829	0.2359
PP10_2	2	PP10	7.935	31.75	FALSE	FALSE	0.324	820.3	0.1247	0.2437	0.007829	0.2359
PP10_3	3	PP10	8.131	32.96	FALSE	TRUE	0.417	820.3	0.1247	0.2437	0.007829	0.2359
PP10_4	4	PP10	10.946	30.62	FALSE	FALSE	0.406	820.3	0.1247	0.2437	0.007829	0.2359
PP10_5	5	PP10	8.639	18.22	FALSE	TRUE	0.761	820.3	0.1247	0.2437	0.007829	0.2359
PP10_6	6	PP10	12.745	24.52	FALSE	TRUE	0.298	820.3	0.1247	0.2437	0.007829	0.2359
PP10_7	7	PP10	13.879	22.05	FALSE	FALSE	0.428	820.3	0.1247	0.2437	0.007829	0.2359
PP10_8	8	PP10	14.466	18.53	FALSE	TRUE	0.650	820.3	0.1247	0.2437	0.007829	0.2359
PP10_9	9	PP10	22.6	25.06	FALSE	TRUE	1.111	820.3	0.1247	0.2437	0.007829	0.2359
PP10_10	10	PP10	20.302	8.816	FALSE	FALSE	3.122	820.3	0.1247	0.2437	0.007829	0.2359
PP10_11	11	PP10	1.786	20.86	FALSE	FALSE	0.276	820.3	0.1247	0.2437	0.007829	0.2359
PP10_12	12	PP10	9.089	15.4	FALSE	TRUE	0.442	820.3	0.1247	0.2437	0.007829	0.2359
PP10_13	13	PP10	5.071	13.17	FALSE	TRUE	0.427	820.3	0.1247	0.2437	0.007829	0.2359
PP10_14	14	PP10	32.64	14.61	FALSE	TRUE	0.826	820.3	0.1247	0.2437	0.007829	0.2359
PP10_15	15	PP10	28.3	15.28	FALSE	TRUE	4.189	820.3	0.1247	0.2437	0.007829	0.2359
PP10_16	16	PP10	32.171	15.52	FALSE	TRUE	0.432	820.3	0.1247	0.2437	0.007829	0.2359
PP10_17	17	PP10	24.897	23.55	FALSE	TRUE	0.300	820.3	0.1247	0.2437	0.007829	0.2359
PP10_18	18	PP10	12.784	35.31	FALSE	TRUE	0.265	820.3	0.1247	0.2437	0.007829	0.2359

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recruit_id	recruit	stone_id	x position	y position	on_cca	on_crevice	dist_to_ cca	stone_area	cca_prop	cre_prop	cre_in_cca_ prop	cre_out_ cca_prop
PP03_1	1	PP03	10.463	13.23	FALSE	TRUE	0.951	601.3	0.1908	0.2985	0.009239	0.2892
PP03_2	2	PP03	8.806	12.88	FALSE	TRUE	0.995	601.3	0.1908	0.2985	0.009239	0.2892
PP03_3	3	PP03	7.719	17.76	FALSE	TRUE	0.242	601.3	0.1908	0.2985	0.009239	0.2892
PP03_4	4	PP03	4.081	20.94	FALSE	TRUE	2.593	601.3	0.1908	0.2985	0.009239	0.2892
PP03_5	5	PP03	3.481	21.13	FALSE	TRUE	3.177	601.3	0.1908	0.2985	0.009239	0.2892
PP03_6	6	PP03	5.731	21.28	FALSE	FALSE	1.324	601.3	0.1908	0.2985	0.009239	0.2892
PP03_7	7	PP03	17.019	21.24	FALSE	FALSE	0.273	601.3	0.1908	0.2985	0.009239	0.2892
PP03_8	8	PP03	8.806	30.36	FALSE	TRUE	0.671	601.3	0.1908	0.2985	0.009239	0.2892
PP03_9	9	PP03	7.269	24.51	FALSE	TRUE	3.334	601.3	0.1908	0.2985	0.009239	0.2892
PP03_10	10	PP03	13.081	24.62	FALSE	TRUE	0.295	601.3	0.1908	0.2985	0.009239	0.2892
PP03_11	11	PP03	6.556	20.08	FALSE	TRUE	0.400	601.3	0.1908	0.2985	0.009239	0.2892
PP03_12	12	PP03	9.744	18.47	FALSE	TRUE	0.387	601.3	0.1908	0.2985	0.009239	0.2892
PP03_13	13	PP03	10.494	14.91	FALSE	TRUE	0.275	601.3	0.1908	0.2985	0.009239	0.2892
PP01_1	1	PP01	18.422	11.01	FALSE	TRUE	0.422	477.9	0.1026	0.2285	0.002970	0.2255
PP01_2	2	PP01	12.471	14.11	FALSE	TRUE	1.869	477.9	0.1026	0.2285	0.002970	0.2255
PP01_3	3	PP01	22.31	16.18	FALSE	TRUE	1.121	477.9	0.1026	0.2285	0.002970	0.2255
PP01_4	4	PP01	29.729	7.287	FALSE	TRUE	2.128	477.9	0.1026	0.2285	0.002970	0.2255
PP01_5	5	PP01	16.895	4.591	FALSE	TRUE	0.256	477.9	0.1026	0.2285	0.002970	0.2255
PP01_6	6	PP01	18.877	5.421	FALSE	TRUE	0.987	477.9	0.1026	0.2285	0.002970	0.2255
PP01_7	7	PP01	11.066	11.6	FALSE	FALSE	0.671	477.9	0.1026	0.2285	0.002970	0.2255
PP33_1	1	PP33	1.987	20.76	FALSE	FALSE	0.212	984.8	0.1012	0.1712	0.001025	0.1702
PP33_2	2	PP33	1.614	16.85	FALSE	TRUE	0.086	984.8	0.1012	0.1712	0.001025	0.1702
PP33_3	3	PP33	8.104	22.84	FALSE	TRUE	0.213	984.8	0.1012	0.1712	0.001025	0.1702
PP33_4	4	PP33	11.813	25.94	FALSE	TRUE	0.910	984.8	0.1012	0.1712	0.001025	0.1702
PP33_5	5	PP33	17.111	37.69	FALSE	TRUE	1.726	984.8	0.1012	0.1712	0.001025	0.1702
PP33_6	6	PP33	24.329	37.39	FALSE	TRUE	0.661	984.8	0.1012	0.1712	0.001025	0.1702
PP33_7	7	PP33	28.601	36.1	FALSE	TRUE	3.165	984.8	0.1012	0.1712	0.001025	0.1702
PP33_8	8	PP33	28.634	38.88	FALSE	FALSE	4.329	984.8	0.1012	0.1712	0.001025	0.1702
PP33_9	9	PP33	18.137	45.84	FALSE	FALSE	1.907	984.8	0.1012	0.1712	0.001025	0.1702
PP33_10	10	PP33	16.217	47.66	FALSE	FALSE	0.272	984.8	0.1012	0.1712	0.001025	0.1702
PP33_11	11	PP33	9.793	2.31	FALSE	TRUE	2.227	984.8	0.1012	0.1712	0.001025	0.1702
PP33_12	12	PP33	5.621	13.3	FALSE	TRUE	0.239	984.8	0.1012	0.1712	0.001025	0.1702

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