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Early life-stage culture of habitat-forming temperate octocorals: Advancing conservation and restoration

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Abstract

Temperate and cold-water gorgonians are important habitat-forming species in coral garden ecosystems, yet their early life stages remain poorly understood, partly because cultivation of sexually produced recruits under aquarium conditions is scarcely established. This limits both experimental studies of recruitment and the development of conservation and restoration approaches.

In this exploratory study, we investigated the longer-term cultivation of sexually produced recruits of the cold-water gorgonian *Paramuricea* sp. We documented early ontogeny and post-settlement survival and growth under different *ex situ* and *in situ* cultivation conditions.

Early development followed a clear sequence, from establishment of primary polyp anatomy through biomineralization and sclerite formation to tentacle development, budding, and onset of colony formation. Post-settlement mortality was particularly high under *in situ* conditions, highlighting early recruitment as a critical demographic bottleneck.

Under aquarium conditions, comparison of three commercially available diets showed that one treatment was associated with higher survival and growth than the other two. Although limited replication prevents causal inference about individual feed characteristics, the results indicate that feeding conditions may strongly influence the cultivation of juvenile azooxanthellate octocorals, which depend entirely on heterotrophic nutrition.

Overall, our results demonstrate that longer-term cultivation of sexually produced *Paramuricea* recruits is feasible and provide a basis for controlled experimental studies and the further development of restoration approaches for temperate and cold-water gorgonians.

1. Introduction

While coral ecosystems rank among the most species-rich environments on earth, many corals themselves are among the largest, oldest, and most ecologically significant organisms ever to have existed; nevertheless, their future remains highly uncertain (Connell 1978; Hoegh-Guldberg et al. 2007; Hughes et al. 2017; Martin-Garin & Montaggioni 2023; Orejas & Jiménez 2017). The ecological importance and biodiversity of coral ecosystems have been increasingly recognized over recent decades, with growing attention also being directed toward cold-water and temperate coral systems, including gorgonian forests. (Freiwald & Roberts 2005; Rossi et al. 2022). These ecosystems can rival their tropical counterparts in ecological importance and ecosystem functioning (Bongiorni et al. 2010; Colletti et al. 2025; Freiwald 2003; Paoli et al. 2015; Roberts et al. 2006). They too have been classified as Vulnerable Marine Ecosystems (VMEs), and their protection is now recognized as a global priority for marine biodiversity conservation (Fao 2009; Orejas et al. 2022).

Their designation as vulnerable reflects their exposure to a range of anthropogenic threats, including pollution, climate change, ocean acidification, and, most prominently, destructive bottom-contact fishing

practices, which can cause large-scale habitat degradation and the loss of habitat-forming coral species (Bavestrello et al. 1998; Bramanti et al. 2023; Garrabou et al. 2022; Hinz 2015). Recovery from such disturbances is particularly limited in many non-tropical species because of their low growth and recruitment rates and long maturation times (Andrews et al. 2002; Andrews et al. 2009; Fava et al. 2010; Prouty et al. 2016; Roberts et al. 2016).

To support recovery in severely degraded systems, active restoration through asexual propagation has become increasingly established, particularly for tropical coral reefs. For non-tropical corals, however, only a limited number of experimental and pilot-scale restoration efforts have been conducted to date (but see Edery et al. 2025; Montseny et al. 2020; Montseny et al. 2021a; Montseny et al. 2021b). In tropical systems, restoration strategies based on sexual reproduction have also received increasing attention (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). These approaches involve rearing sexually produced larvae and recruits under controlled conditions and subsequently transplanting them into degraded habitats, thereby maintaining genetic diversity and potentially enhance adaptive capacity (Chamberland et al. 2015; Henry et al. 2021; Petersen & Tollrian 2001).

The success of such restoration strategies, however, critically depends on processes occurring during early life stages. In tropical corals, larval settlement, substrate selection, early ontogeny, and post-settlement survival and growth are known to be key determinants of population dynamics (Caley et al. 1996; Hughes & Tanner 2000; Ritson-Williams et al. 2010). The early recruit phase, in particular, represents a major demographic bottleneck marked by high mortality rates (Penin et al. 2010; Vermeij & Sandin 2008). Survival during this stage is strongly influenced by factors such as microhabitat structure, food availability, and environmental stress (Doropoulos et al. 2016). In addition, conditions experienced during early development can have long-lasting effects on organismal fitness through so-called carry-over effects (Doropoulos et al. 2015; Edmunds 2007). Accordingly, various approaches have been explored to enhance recruitment success, including optimized feeding regimes (Rodd et al. 2022; Toh et al. 2014) ; Despite these advances, comparable restoration approaches based on sexual reproduction have not yet been established for temperate and cold-water corals, although recent studies have made progress in this direction (e.g. Egger et al. 2025; Giordano et al. 2026a). Importantly, many cold-water and temperate corals, particularly azooxanthellate octocorals, differ fundamentally from tropical scleractinian corals in their nutritional physiology, developmental timing, and habitat requirements, meaning that restoration approaches developed for tropical corals cannot be directly transferred to these systems (Bramanti et al. 2026; Cocito et al. 2013; Ribes et al. 1999; Roberts et al. 2006). To date, even maintaining cold-water and temperate gorgonians under optimal aquarium conditions remains highly challenging, largely because of limited knowledge of their biological and ecological requirements (Orejas et al. 2019). Although progress has been made in understanding nutritional requirements, larval settlement cues, and substrate preferences of temperate gorgonians, (Egger et al. 2026b; Giordano et al. 2026b; Manea et al. 2025; Rossi et al. 2006; Rossi & Rizzo 2021; Viladrich et al. 2016), considerably less is known about early post-settlement stages, including the ecological requirements of recruits. This knowledge gap hampers the design of targeted experiments and the development of ex situ culture

protocols, while also limiting the development of effective restoration strategies aimed at promoting population recovery through sexually produced corals.

Therefore, this study investigates the early-life ecology of an important habitat-forming Atlantic gorgonian of the genus Paramuricea occurring off the west coast of Portugal. The as-yet undescribed species is closely related to its Mediterranean sister species, *Paramuricea clavata* (Coelho et al. 2023; Egger et al. 2026a; Egger et al. in prep.) and is subject to substantial fishing pressure (Dias et al.). We tracked early ontogeny and assessed the survival and growth of sexually produced recruits under controlled aquarium/ex situ conditions across different feeding regimes, as well as under field/*in situ* conditions.

2. Methods

2.1 Coral collection, larvae rearing, and settlement

The sexually produced recruits of a *Paramuricea* sp. used in this study originated from several spawning cohorts between August 3rd and September 9th, 2024, and from subsequent settlement experiments. The parent colonies were collected between July and August 2024 as bycatch from bottom-set fishing nets near Cape St. Vincent in Sagres, Portugal. The colonies were maintained at the Ramalhete Marine Station in Faro in a temperature-controlled (15–16°C), partially recirculating indoor aquarium system in 150-L tanks. Negatively buoyant eggs, embryos, and larvae were gently siphoned from the bottom of the tank during spawning. They were transferred to 1-L containers and maintained under the same temperature conditions, with gentle aeration and 50% water exchange every two days (for details on collection sites and spawning conditions, see Egger et al. 2026a). The larvae were subsequently exposed to different substrate types And settlement occurred predominantly on rocks from their natural habitat that were colonized by crustose coralline algae (CCA) (for details on settlement see Egger et al. 2026b).

2.2 Recruit development

To estimate the average timing of the development of major morphological features, including the mouth opening, mesenteries (partitions separating the eight compartments of the polyp), tentacles, pinnules (small, radially arranged projections of the tentacles), sclerites (needle-like skeletal elements embedded within the surface tissue), and pigments (strongly colored granules that were clearly distinguishable from the surrounding tissue and appeared only after some time in the recruit tissue, but whose chemical composition and function are currently unknown), 76 settled individuals were examined every 1–2 days during the first 10–14 days after settlement and at longer intervals thereafter (see Supplementary Table 1). At each examination, recruits were counted and photographed at 30× magnification using a Zeiss Stemi stereomicroscope equipped with an Axiocam camera. Developmental features were subsequently scored from the images as present (1), absent (0), or not visible (NA).

To determine the first occurrence of each feature, we used a status-based interval-censored estimator (e.g. Syrjälä et al. 2021; Taylor 2019). For each polyp and each feature, the earliest confirmed occurrence

was defined as the first observation scored as “1”. The developmental window was then defined as the interval between the last preceding observation scored as “0” (*window start*) and the first confirmed occurrence (*window end*). Because observation frequency decreased during developmental later stages, window sizes were corrected by applying a feature-specific upper limit based on the 90th percentile. The most likely day of occurrence was calculated as the midpoint (days after settlement), with uncertainty expressed as half the corrected window size. The sample size (N) therefore represents the number of polyps in which the respective feature could be reliably detected. Sample sizes varied among features (N = 47–76), with fewer observations available for developmental features appearing later because of recruit mortality.

Because some recruits were used after approximately two months in the subsequent experiments involving different treatments, features that appeared only after this period, enlargement of the basal region, budding, and axis formation, were described qualitatively only.

2.3 Survival and growth of recruits under different treatments

A total of 138 recruits on 32 substrate pieces that had already developed into primary polyps were selected and, on 20 October 2024, assigned either to three ex situ feeding treatments under culture conditions (76 recruits) or, for comparison, to a natural environmental context through transplantation to an *in situ* field nursery (62 recruits; Table 1). Each substrate and each recruit was assigned a unique identifier (ID). Recruits in the *ex situ* treatments were maintained in three 60-L indoor aquaria under the same conditions as the adult colonies, except for the food supply. Each aquarium was continuously supplied with food over 24 h per day using automated dosing pumps. Each tank received a different commercially available, ready-to-use feed containing small particles < 100 µm, corresponding to the small size of the recruits (Table 1).

Because some Mediterranean temperate gorgonians are suspension feeders capable of exploiting a broad spectrum of organic food sources (Cocito et al. 2013; Ribes et al. 1999), we deliberately selected feeds that differed substantially in the type of nutritional material they provided and that had been developed for aquaculture applications. Twenty-seven recruits were fed *Zootonic* (Tropic Marin), a liquid formulation containing dissolved nutrients; 26 recruits received *EasyBooster* and *EasyFarm* (referred to as *EasyReef*), a microalgae-based feed. Both products are commonly used in the tropical aquarium trade as complete feeds for tropical corals. The remaining 23 recruits were fed *Zebrafeed* (Sparos), a particulate feed (Table 1) that, like *EasyReef*, was specifically formulated for rearing juvenile organisms, although it was originally developed for zebrafish larvae in biomedical research. Feeding rates were determined in preliminary trials to establish the maximum daily dose that could be administered without adversely affecting water quality in the aquaria or the connected aquarium systems.

Table 1
Feeding product with description, ingredients, and the dosage used to assess the best *Paramuricea* sp recruit feed.

Because the number of available recruits was limited, each treatment was represented by only a single aquarium (n = 1), meaning that treatment effects may be confounded with tank-level differences. In addition, despite several filtration stages, the aquarium systems remained interconnected, such that some exchange of nutrients among systems could not be completely excluded. Group sizes were not identical because the number of recruits per stone varied. Nevertheless, we attempted to balance treatments by distributing stones with different recruit densities randomly but as evenly as possible among treatments (e.g. stones with few [2, 3, etc.] or many [> 10] recruits were represented in all treatments; see also **Table S3**). Initial recruit densities were compared using a Kruskal–Wallis rank-sum test to assess whether initial recruit numbers differed among treatments.

For comparison with the natural environmental context (*in situ*), 14 substrate pieces were mounted on four plastic plates (15 × 20 cm), which were subsequently attached to a larger plastic plate (1 × 1 m). This plate was secured to natural rock beneath an overhang in Sagres harbor (37.012028, − 8.924694) at a depth of 14 m. Deployment was carried out by SCUBA divers on 20 October 2024. For monitoring, the four smaller plastic plates were unscrewed, transferred to sealed transport containers, and photographed at the surface using a Zeiss Stemi stereomicroscope equipped with an Axiocam camera. After examination, the substrates were returned to their original field location.

Monitoring of both the *in situ*-transplanted and *ex situ*-cultured recruits was conducted at approximately the same time whenever possible, depending on whether field conditions permitted diving. Baseline monitoring was conducted before initiation of the different feeding treatments and field deployment, between 17 and 20 October 2024 (**T0**). Subsequent monitoring was conducted 20–28 days (**T1**), 117–134 days (**T2**), and 180–201 days (**T3**) after T0. Subsequently, all remaining ex situ recruits were switched to the *Zebrafeed* diet and examined again after 283–286 days (**T4**). At each monitoring time point, recruits were individually counted and photographed, predominantly at 30× magnification as described above. Qualitative observations of behavior and food uptake during exposure to the different feeds were documented simultaneously.

2.3.1 Recruit survival

Separate survival curves were calculated for each treatment using the Kaplan–Meier estimator implemented in the R package survival. Because Kaplan–Meier estimation assumes independent observations and exact event times, whereas recruits originating from the same settlement stone were not independent and mortality was recorded only at discrete monitoring time points, Kaplan–Meier analysis was used exclusively for descriptive visualization.

Statistical comparisons among treatments were performed using a generalized linear mixed-effects model (GLMM) with a binomial error distribution and logit link function. To account for repeated observations while simultaneously avoiding pseudoreplication following mortality events, the data were converted into interval-based survival data. For each stone and each sampling interval (T0–T1, T1–T2, T2–T3, and T3–T4), the numbers of surviving and dead recruits were calculated, and survival during each interval was modelled as the proportion of recruits surviving that respective interval. The model included treatment and sampling interval as fixed effects and stone identity as a random intercept to account for the non-independence of recruits originating from the same settlement stone:

$\text{cbind}(\text{Alive}_{\text{end}}, \text{Deaths}) \sim \text{Treatment} + \text{Interval} + (1|\text{StoneID})$

The model was fitted using the glmer() function from the R package lme4 in RStudio (version 2026.01.2), and model convergence was achieved using the bobyqa optimizer with an increased maximum number of iterations. Overall effects of treatment and interval were assessed using Type II Wald χ^2 tests. Subsequent pairwise comparisons among treatments and intervals were based on estimated marginal means with Tukey-adjusted P-values (emmeans package). Model fit was assessed by inspection of residuals and tests for overdispersion.

2.3.2 Recruit size (growth)

To track and compare changes in the size of individual polyps over time, images were standardized to the same magnification (3×), and the measurement tool in Adobe Photoshop 22.2.0 was calibrated before being used to measure the diameter of the crown region of the polyp (*sensu* Bayer 1983; Fig. 1a). In total, 124 individuals on 32 stones were followed, resulting in 303 measurements (see **Table S6**). To determine whether the measured size of the polyp crown region was affected by polyp expansion or imaging angle, seven different recruits were photographed with their tentacles extended and retracted, with retraction induced by touching the recruit, and/or from different viewing angles. Two to four images were obtained and measured for each recruit and subsequently compared (Fig. 1). The standard deviation and standard error of these measurements were calculated for each recruit. Across the seven example recruits, the mean standard deviation was 10.6 µm and the mean standard error was 7.0 µm, corresponding to approximately one-fifth of the standard deviation observed across all recruit measurements and to 2.0% and 1.3% of the mean recruit size, respectively. This measurement variability was considered sufficiently low to justify the use of the proposed method. Budding (i.e. the presence of two polyps within a single individual) was accounted for by summing up the measurements of the two individual polyps.

To test whether recruit size differed among the four treatments and whether initial recruit size or stone of origin had an effect, a linear mixed-effects model (LMM) with a repeated-measures design was used, incorporating random effects for individuals and stones:

$$Growth_{ij} = \beta_0 + \beta_1 (Treatment_i) + \beta_2 (Time_j) + \beta_3 (Food_i \times Time_j) + (1| Stone_k/Individual_l) + \varepsilon_{ijkl}$$

The main model was restricted to the experimental period before the treatment conditions were switched to *Zebrafeed* (**T3–T4**) and was fitted using the lmer function. The significance of fixed effects was assessed using a Type III ANOVA, followed by Tukey-adjusted pairwise comparisons of estimated marginal means.

3. Results

3.1 Recruit development

Developmental windows and the calculated mean timing of the first appearance of individual morphological features differed markedly among traits (see **Figure S 1** and **Table S 2**). The most probable sequence of development was as follows:

The mouth opening (Fig. 2b) and internal compartmentalization by the mesenteries (Fig. 2c) developed within the first day after settlement (0.6 d mean interval midpoint ± 0.5 d mean uncertainty, based on N = 76 evaluated recruit images; and 0.9 ± 0.5 d, N = 74, respectively; see also the developmental windows provided in **Figure S1**). Sclerites (Fig. 2d) and tentacles (Fig. 2e) most likely developed around day 4 (3.7 ± 1.0 d, N = 67, and 4.1 ± 1.1 d, N = 62, respectively). Active feeding, defined as the transport of food particles by the tentacles towards the mouth opening, was first observed after the development of the feather-like pinnules (Fig. 2f) (12.1 ± 4.5 d, N = 55).

Although coral larvae and early recruits already exhibited a deep purple coloration, they developed large, approximately 10-µm magenta-coloured granules considerably later than the other morphological features (22.9 ± 7.5 d, N = 47; Fig. 2g). As described above, these granules were referred to as pigments and are also present in adult colonies.

The recruits subsequently increased in both body and sclerite size (Fig. 2h) and consistently enlarged their basal, substrate-attached area (Fig. 2i), before budding of a second polyp was observed (Fig. 2j). Formation of the gorgonin-containing axial skeleton was not observed, even after budding had occurred.

3.2 Recruit survival and growth under different treatments

3.2.1 Recruit survival

Survival differed significantly among treatments (Type II Wald $\chi^2 = 17.93$, df = 3, $p < 0.001$, Fig. 3) and monitoring intervals ($\chi^2 = 48.55$, df = 3, $p < 0.001$; **Table S 5** and **Table S 6**), while the initial number of

recruits per settlement stone did not differ significantly among treatments (Kruskal–Wallis: $\chi^2 = 1.51$, df = 3, p = 0.681). Model diagnostics indicated no evidence of overdispersion (dispersion ratio = 1.06, p = 0.536), while residual variation among settlement stones was relatively modest (random-intercept SD = 0.454).

Pairwise comparisons showed significantly greater interval survival under *Zebrafeed* than under *EasyReef* (p = 0.027), and *Zootonic* (p = 0.005) and under field conditions (p < 0.001), whereas the remaining pairwise comparisons were not significant (**Table S 8**).

Cumulative survival declined substantially over time in all treatments, although the magnitude of the decline differed markedly among treatments (Fig. 3 and **Table S 4**). At **T1**, 100% of *Zebrafeed* recruits remained alive, compared with 93% under *Zootonic*, 88% under *EasyReef*, and 84% under field conditions. By **T2**, survival remained high under Zebrafeed (91%) but had declined to 50% under *EasyReef*, 41% under *Zootonic*, and 34% under field conditions. At **T3**, 52% of the initial *Zebrafeed* recruits remained alive, compared with 23% under *EasyReef*, 19% under *Zootonic*, and only 8% under field conditions. After all remaining *ex situ* recruits were transferred to the *Zebrafeed* diet, cumulative survival in the former *EasyReef* and *Zootonic* groups continued to decline, reaching 12% and 4% at **T4**, respectively, whereas survival in the former *Zebrafeed* group remained unchanged at 52%.

3.2.2 Recruit growth

Recruit growth was strongly influenced by treatment, time, and their interaction (Type III ANOVA: treatment, $F_{3,22.61} = 71.94$, p < 0.001; time, $F_{3,199.90} = 118.98$, p < 0.001; treatment × time, $F_{9,198.16} = 41.97$, p < 0.001), indicating treatment-specific growth trajectories over time (Fig. 4; **Table S 8**).

At the start of the experiment (T0), recruit crown diameter did not differ significantly among treatments (mean ± SD: 299 ± 51.2 µm; **Table S 7**: all post hoc pairwise comparisons p > 0.05). By T1, *field* recruits were significantly larger than recruits maintained under the *Zootonic* treatment (384 ± 64.2 vs. 304 ± 47.4 µm; p = 0.003), whereas *EasyReef* and *Zebrafeed* recruits exhibited intermediate sizes and did not differ significantly from either treatment. *Zootonic* recruits also did not differ significantly from *EasyReef*.

At T2, differences among treatments became more pronounced. *Field* recruits attained the largest crown diameter (563 ± 104 µm), followed by *Zebrafeed* recruits (448 ± 76.4 µm), whereas recruits maintained under *EasyReef* (325 ± 49.4 µm) and *Zootonic* (296 ± 41.6 µm) remained significantly smaller than those in both of the former treatments (all p < 0.001), but did not differ from one another (p = 0.997). This pattern became even more pronounced by **T3**: *field* recruits reached a crown diameter of 940 ± 196 µm, followed by *Zebrafeed* recruits at 577 ± 84 µm, whereas *EasyReef* and *Zootonic* recruits remained comparatively small (325 ± 49.4 µm and 327 ± 41.1 µm, respectively; all pairwise comparisons with *field* and *Zebrafeed*, p < 0.001).

After all *ex situ* recruits were transferred to the *Zebrafeed* diet after T3, recruits previously maintained under *Zebrafeed* continued to increase in diameter, whereas only one surviving recruit from the former

EasyReef treatment could be reliably measured at **T4** and showed no appreciable increase in size (Fig. 4) (Fig. 4, T4).

3.3 Feeding behavior

In addition to the different survival and growth trajectories observed under the different feeding regimes, recruits also appeared to exhibit distinct behavioural responses to the respective feeds. Although these observations were not quantified systematically, recruits exposed to *Zebrafeed* showed noticeably increased tentacle activity. Larger *Zebrafeed* particles were captured by the tentacles, manipulated and transferred towards the mouth, and subsequently transported into the gastric cavity by peristaltic movements (see **Video 1**). In contrast, recruits exposed to the finer-particle *Zootonic* feed, as well as to *EasyReef*, showed little apparent increase in tentacle movement following food addition. Instead, the tentacles often became shorter and broader, while the mouth opened (partly visible in **Video 2)**

4. DISCUSSION

This study provides a detailed account of the development and early life stages of an eastern Atlantic temperate gorgonian and investigates the effects of feeding and rearing conditions on survival and growth, aspects that remain poorly documented for non-tropical corals.

4.1 Ontogenetic development of polyp morphology, feeding capacity, and colonial growth

The pronounced differences in the timing of individual developmental traits indicate a functionally ordered ontogeny: the basic polyp body plan is established first, followed by investment in feeding capacity, structural reinforcement, and ultimately modular colonial growth through the formation of additional polyps. In our recruits, the formation of the mouth opening and mesenteries, establishing the internal compartmentalization of the polyp, within the first day after settlement suggests that internal organization and gastrovascular function are established at an early stage. This is consistent with observations in other forest-forming octocoral species, including *Eunicella verrucosa* (Egger et al. 2025), *Dentomuricea* aff. *meteor* (Rakka et al. 2021), and *Eunicella singularis* (Weinberg & Weinberg 1979).

Sclerites and tentacles generally appeared around day four, with sclerite formation slightly preceding tentacle development. This sequence suggests that early recruits may initially prioritize mechanical stability and protection before developing fully functional feeding structures. Early biomineralization may therefore be important for survival during the early post-settlement phase, when recruits are particularly vulnerable to predation and environmental stressors (Bennett et al. 2024). In other octocorals, sclerite development has been reported to begin later, for example in the temperate *Corallium rubrum* (~ 12 days, Giordano et al. 2023) and the tropical *Plexaura homomalla* (~ 7 days, Tonra et al. 2021). Both species, however, differ substantially in their skeletal properties (*C. rubrum*), and habitat (*P. homomalla*). Although

the observed timing may also be influenced by rearing conditions, these comparisons nevertheless indicate interspecific variation in early life-history strategies.

Active feeding, defined here as the transport of food particles towards the mouth by the tentacles, was observed only after complete tentacle development, including the formation of the feather-like lateral pinnules, although tentacle movement was already evident beforehand. This suggests that the presence of tentacles alone may not confer full trophic functionality and is consistent with previous studies showing that feeding efficiency in octocorals depends on the functional maturation of both tentacles and pinnules (Fabricius et al. 1995; Rossi et al. 2017). Other forms of food uptake may, however, have occurred earlier, for example through movements of the ciliated peristome (oral field) in combination with an open mouth. Similar behaviour was observed in older recruits following the addition of dissolved or very fine particulate feeds, such as *Zootonic* and *EasyReef*, where active particle-capture mechanisms may not have been required.

Pigment production, specifically the production of magenta-coloured granules, occurred substantially later than all other early traits and is therefore unlikely to play an important role in immediate settlement success. Conversely, pigment synthesis may represent a considerable energetic investment that can only be sustained once heterotrophic nutrition has been established over a longer period (Koneru & Caro 2022). The delayed appearance of pigments may reflect functions in defence (Thoms & Schupp 2008), buffering of oxidative stress (Palmer et al. 2009), or metabolic processes (Maoka 2011) that become increasingly important or functionally relevant during later post-settlement development.

The transition to colonial growth occurred only after several months, with recruits initially investing in expansion of the basal attachment area before budding commenced. This delayed transition is consistent with developmental trajectories reported for other temperate gorgonians (Egger et al. 2025; Weinberg & Weinberg 1979), although under more favourable conditions budding might potentially begin earlier than observed here. More generally, both aquarium and field conditions may have been suboptimal in some respects and handling could have stressed the recruits, which might therefore have delayed the timing of developmental transitions. The absolute timing of individual developmental events should consequently be regarded as potentially variable rather than fixed. Future experiments conducted under different environmental and husbandry conditions could test if and to what extent variability is present. Such experiments could also determine whether the developmental sequence itself remains conserved. We consider this likely, given the apparent functional order of the observed transitions and the possibility that their sequence is developmentally, and at least partly genetically, constrained.

4.2 Food quality and habitat context effects on early survival and growth

The low overall survival rate (19% after five months) aligns with well-documented patterns of high early post-settlement mortality in benthic invertebrates, including octocorals, for which losses of 70–90% during the first months are common (Gosselin & Qian 1997; Linares et al. 2008; Penin et al. 2011; Vermeij & Sandin 2008).

Post-settlement mortality was particularly high under experimental field conditions, underscoring the early recruitment phase as a critical demographic bottleneck. However, neither the aquarium nor the field nursery fully replicated the natural habitat of the parental colonies, which originated from depths of approximately 40 m. Moreover, it remains unknown whether larvae would naturally have selected settlement sites comparable to those used for nursery deployment. The lower survival observed in the field treatment may therefore partly reflect a mismatch between the experimental nursery environment and the natural recruitment habitat rather than intrinsic differences between ex situ and natural conditions.

Nevertheless, does the lack of evidence for density-dependent mortality, together with the pronounced differences between field and aquarium treatments, suggests that survival was more strongly influenced by environmental conditions, including food availability, habitat conditions, and microhabitat quality, than by density-dependent biotic interactions among recruits. Field-deployed recruits grew more rapidly despite experiencing higher mortality, suggesting a strong dependence on, and potentially a trade-off between, resource availability and environmental stress. Natural food sources in the field likely provide a broader and potentially more suitable spectrum of nutrients for recruits and may thereby promote faster growth. At the same time, however, recruits in the field are exposed to greater sedimentation, hydrodynamic stress, microbial loads, and predation than under aquarium conditions. Similar trade-offs are likely to occur among different microhabitats in natural environments, highlighting the strong influence of habitat conditions on post-settlement survival (Adjeroud et al. 2015; Mumby 1999).

The variation in survival among individual settlement stones within treatments may partly reflect fine-scale habitat heterogeneity, including differences in surface structure, biofilm composition, and microbial communities, factors known to influence not only settlement but also post-settlement survival (Doropoulos et al. 2016; Green et al. 2010). Only natural substrates were used in the present study because larval settlement could only be successfully achieved on such substrates. Consequently, the settlement stones necessarily differed in some of the above-mentioned characteristics, and these differences may have contributed substantially to variation in survival and potentially amplified differences among treatment groups. To separate these substrate-related effects from treatment effects, future experiments would require successful settlement on standardized substrates. An additional limitation that must be considered when interpreting the treatment effects is the lack of independent tank replication resulting from the limited number of available recruits.

Because feeding treatment and aquarium identity were necessarily confounded, our feed results should be interpreted as evidence that at least one rearing condition associated with *Zebrafeed* promoted superior recruit performance. Replicated experiments are required to determine whether the observed effect results directly from dietary composition or from unidentified tank-level characteristics. Furthermore, growth could only be measured in surviving recruits. Treatment-specific mortality may therefore have introduced survivorship bias, because growth measurements represented the more resistant surviving individuals rather than the original cohort as a whole. Growth results should consequently be interpreted as conditional on survival.

Nevertheless, under the aquarium conditions tested here, recruits maintained under the *Zebrafeed* treatment showed substantially higher survival and growth than those maintained under the other feeding treatments. Possible explanations could be nutrient composition, particle size, food concentration, microbial effects, better uptake etc. which should be disentangled in subsequent studies. The contrasting growth trajectories among treatments could further indicate that a more suitable nutritional regime, as apparently provided under field conditions and, to some extent, possibly by *Zebrafeed*, allows recruits to allocate more energy to growth. Under less suitable feeding conditions, such as the *Zootonic* and *EasyReef* treatments, energy allocation may instead have been largely restricted to maintenance and survival, resulting in limited biomass accumulation.

In contrast to several tropical octocoral species whose nutrition relies substantially on phytoplankton (Fabricius et al. 1995), an exclusively phytoplankton- or nutrient- based diet (*EasyReef* and *Zootonic*) could have been insufficient for recruits of this azooxanthellate octocoral under the conditions of our study. Recruits maintained under the *Zebrafeed* treatment also displayed different feeding behaviour, actively capturing the comparatively larger food particles. This possibly suggests that not only nutrient composition but also particle size and/or digestibility may be important determinants of feeding success. Alternatively, or additionally, these observations may indicate that recruits are able to adjust their feeding behaviour in response to differences in food availability, as has been reported for some cold-water corals (Van Oevelen et al. 2016).

Such a dependence on particle characteristics also appears plausible in the context of the known trophic ecology of temperate gorgonians. Several temperate Mediterranean gorgonians can exploit a broad range of organic food sources, including zooplankton, particulate organic matter (POM), and sedimentary organic matter (SOM) (Cocito et al. 2013; Ribes et al. 1999), but the range of particles they can effectively utilize is constrained by tentacle and pinnule morphology as well as by their ingestion and digestive capacities. These limitations are likely to be particularly pronounced in early recruits because of their small body and polyp size. For example, the sympatric and likewise small-polyped gorgonian *Leptogorgia sarmentosa*, predominantly feeds on particles of approximately 3.6–200 µm (Ribes et al. 2003; Rossi et al. 2004), whereas adult polyps of *Paramuricea clavata* can ingest copepods up to approximately 700 µm in size (Ribes et al. 1999). Prey of this size would, however, likely be beyond the capture capacity of early recruits measuring only approximately 250–500 µm. Taken together, this possibly suggests that successful rearing of early *Paramuricea stages* may depend not only on nutritional quality, but also on providing a suitable particle-size spectrum.

The continued high mortality in the former *Zootonic* and *EasyReef* groups, even after transfer to *Zebrafeed*, may further indicate delayed carry-over effects of suboptimal early nutritional conditions, as previously described for early life stages of other corals (Doropoulos et al. 2015; Doropoulos et al. 2016; Edmunds 2007). In this context, the pronounced individual variation in recruit growth may also be consistent with the possibility that early differences in physiological condition and settlement history have persistent effects on subsequent recruit performance. This may be particularly relevant because larger recruits generally experience lower mortality (Doropoulos et al. 2016; Penin et al. 2010).

4.3 Concluding implications for conservation and restoration

The high-resolution developmental timeline presented here provides a valuable framework for future studies examining how environmental conditions and husbandry practices influence the timing of developmental transitions.

The very high mortality observed during the early benthic phase, with only 8% survival under field conditions after six months, suggests that post-settlement survival may represent a major demographic bottleneck. For the natural recovery of degraded coral populations, this implies that recruitment may not be limited solely by larval supply or connectivity, but also, and potentially more strongly, by the survival of newly settled recruits. This is particularly relevant for recovery following physical disturbance, such as bottom trawling, because even where larval connectivity is sufficient, only a small fraction of settlers may ultimately contribute to population replenishment. High post-settlement mortality may therefore constrain local population recovery, as well as the resilience and long-term persistence of coral forests. Under changing environmental conditions, this bottleneck could become even more important if thermal stress, sedimentation, or other climate-related pressures further reduce survival during these already vulnerable early life stages.

In addition, the pronounced sensitivity of recruits to food quality under the present aquarium conditions and to environmental stress under field conditions may underscore the vulnerability of early life stages to changes in marine primary productivity and trophic regimes. Environmental changes that reduce food availability or alter the composition of available particles could therefore have substantial consequences for population maintenance, even in the absence of direct physical disturbance.

Our preliminary findings may also serve as a first step towards the development of aquarium-based research approaches. Such approaches could, for example, support experimental investigations of early life-stage ecology, contribute to conservation assessments, and facilitate the development of restoration strategies for temperate octocorals. Because early nutritional deficits can potentially result in persistent reductions in later performance, nutritionally appropriate feeding during early ontogeny may help to produce healthier recruits that more closely resemble naturally developed juveniles and thereby improve the reliability of subsequent experiments. Although our results require further experimental validation, they suggest, as discussed above, that the nutritional requirements of recruits of this temperate octocoral may, similar to those of adult colonies, differ substantially from those of tropical octocoral species. Meeting these requirements has so far often involved considerable effort associated with the cultivation of live feeds. The apparent positive response of our recruits to one of the commercial feeds tested may indicate that formulated feeds with appropriate nutritional profiles could provide a practical and less labour-intensive alternative to live-food cultures.

Of relevance to restoration is the fact that the juveniles cultured in this study were produced through sexual reproduction. Many current coral restoration approaches rely predominantly on fragmentation,

transplantation, or other forms of asexual propagation (Boström-Einarsson et al. 2020; Edery et al. 2025; Montseny et al. 2020). Although these methods can enable the rapid propagation of existing genotypes, they do not directly increase the genetic diversity of restored populations. In contrast, the use of sexually produced recruits provides an opportunity to introduce new genetic combinations into restoration efforts and, provided that a sufficiently large and genetically representative number of parent colonies is included, may help to maintain the genetic diversity and evolutionary potential of restored populations (Suggett et al. 2022; van Oppen et al. 2015). This may become particularly relevant under ongoing climate change, as maintaining standing genetic variation, particularly heritable variation in environmentally relevant traits, provides the basis for natural selection and may therefore enhance the adaptive potential of restored populations (Torda et al. 2017; Baums et al. 2019; DeFilippo et al. 2022). A better understanding of the ecological and nutritional requirements of early life stages under controlled conditions is therefore important not only for experimental research, but also as a prerequisite for the development of sexual restoration approaches. In tropical coral reefs, methods for rearing and deploying sexually produced recruits are increasingly being developed as a complement to fragment-based restoration techniques (Banaszak et al. 2023; Chamberland et al. 2017, dela Cruz & Harrison 2017). Comparable approaches remain not yet established for temperate and cold-or temperate octocorals, also because their physiology and requirements differ fundamentally (Bramanti et al. 2026). The ability to reliably culture sexually produced early life stages in larger numbers could therefore provide an important foundation for future restoration efforts. Improving post-settlement survival and growth through appropriate feeding regimes could increase the reliability of aquarium-based experiments while also representing an important step towards scalable restoration strategies based on sexually produced recruits.

Declarations

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Figures

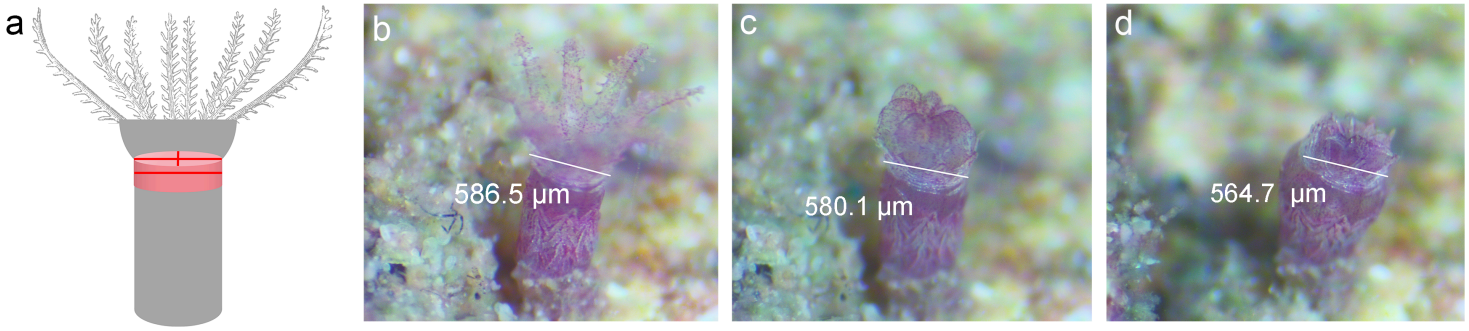


Figure 1

Figure 1 Measuring the crown region of primary polyps to compare recruit sizes in purple *Paramuricea* sp. (**a**) shows the different measurement axis that can be used to achieve a similar result. (**b-d**) shows the same recruit with tentacles extended, retracted and full body retraction. The neck region remains approximately the same size.

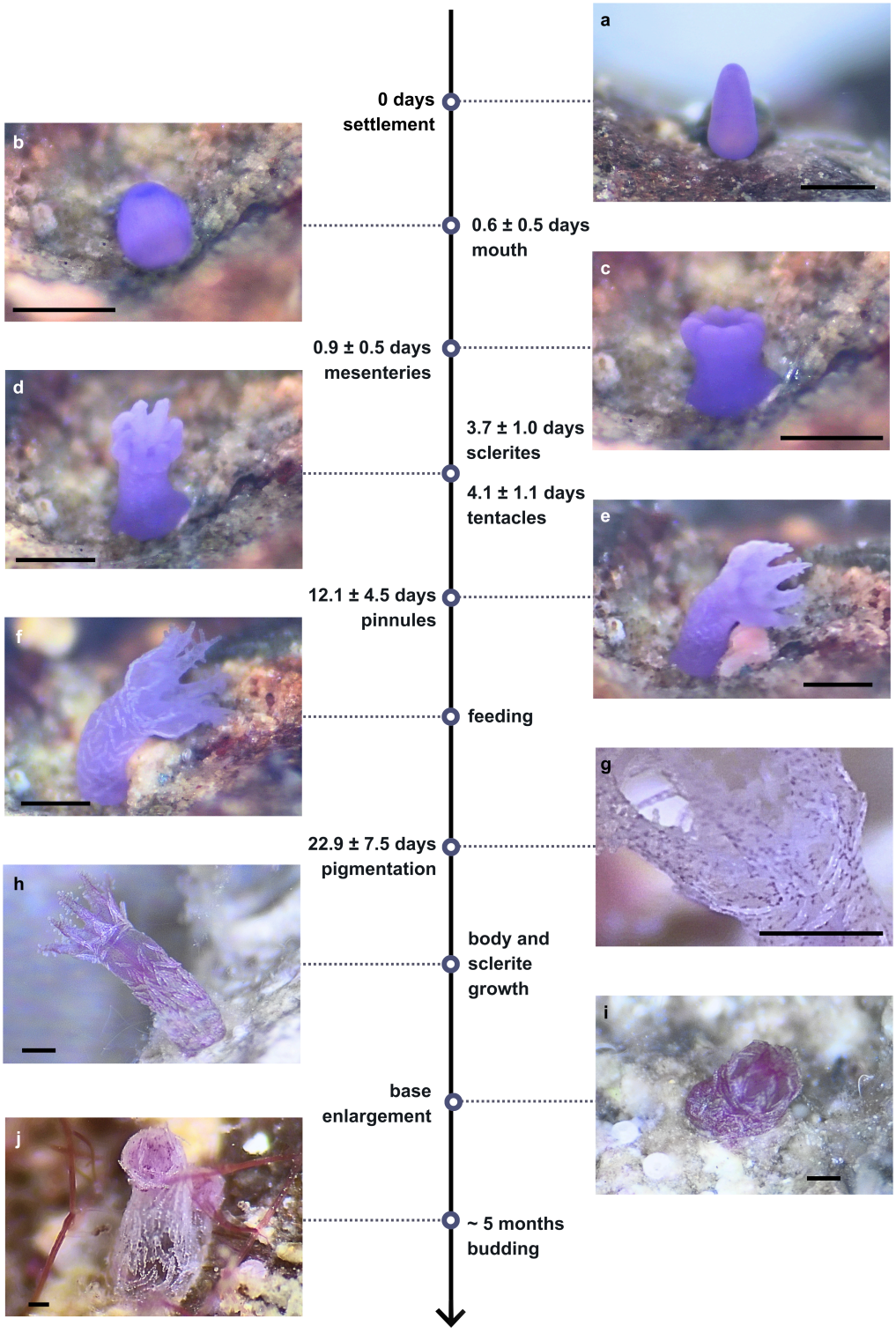


Figure 2

Figure 2 Development timeline after settlement of *Paramuricea* sp. coral recruit (**a**) of the average first occurrence ± uncertainty of mouth (**b**), mesenteries (**c**), sclerites (**d**), tentacles (**d**, **e**), pinnules (**e**, **f**) and pigmentation (**g**). Growth (**h**), base enlargement (**f**) and budding (**j**) were observed within the first five months of recruit life. Scale bars: 500 µm.

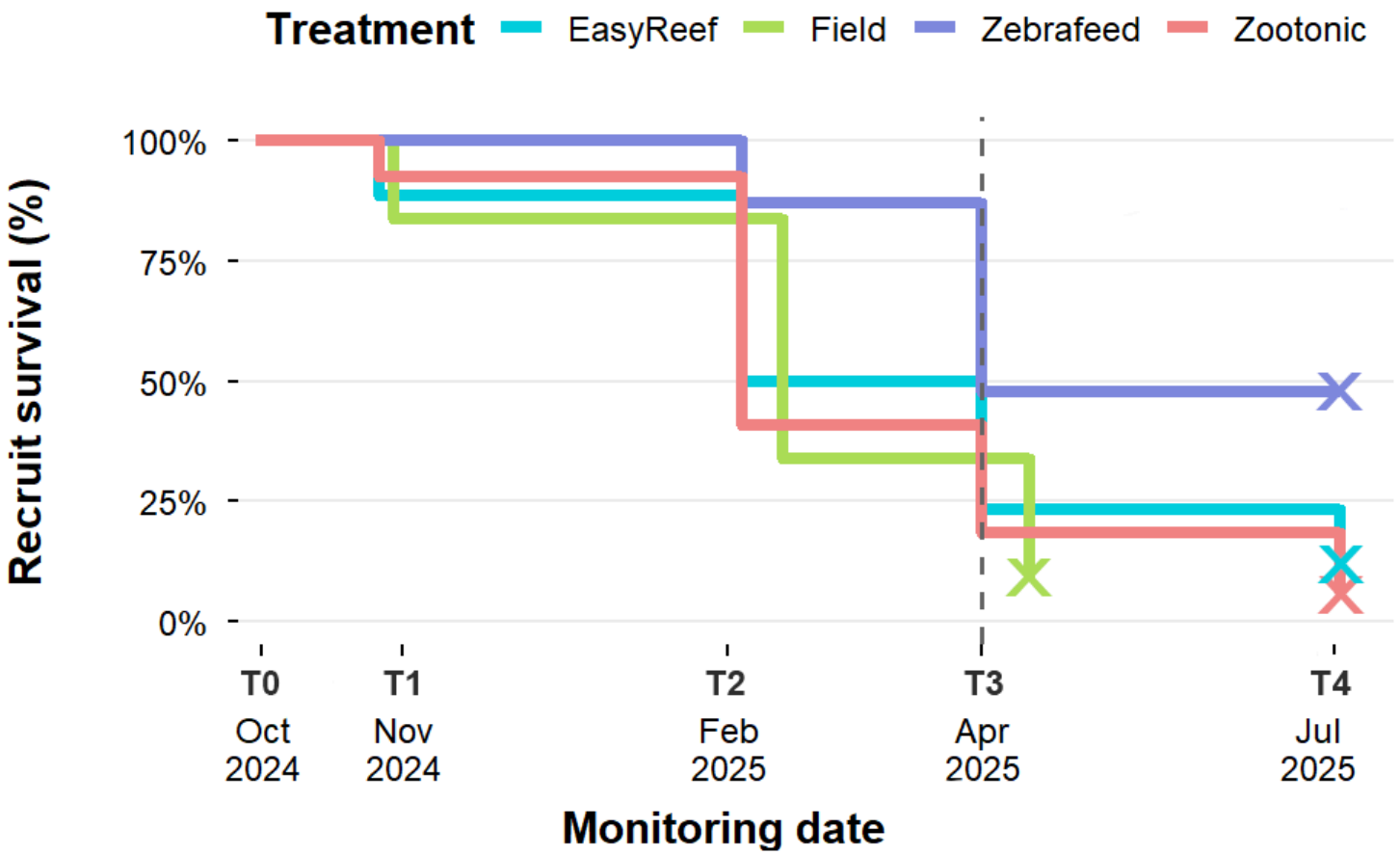


Figure 3

Figure 3 Kaplan–Meier survival curves of individually monitored *Paramuricea* recruits across three experimental feeding treatments (*EasyReef*, *Zebrafeed* and *Zootonic*) over time and recruits incubated *in situ* (*field*). *EasyReef*, *Zebrafeed* and *Zootonic* The dashed vertical line indicates the end of the experimental feeding treatments (**T3**), after which all surviving aquarium recruits were maintained under a common *Zebrafeed* feeding regime.

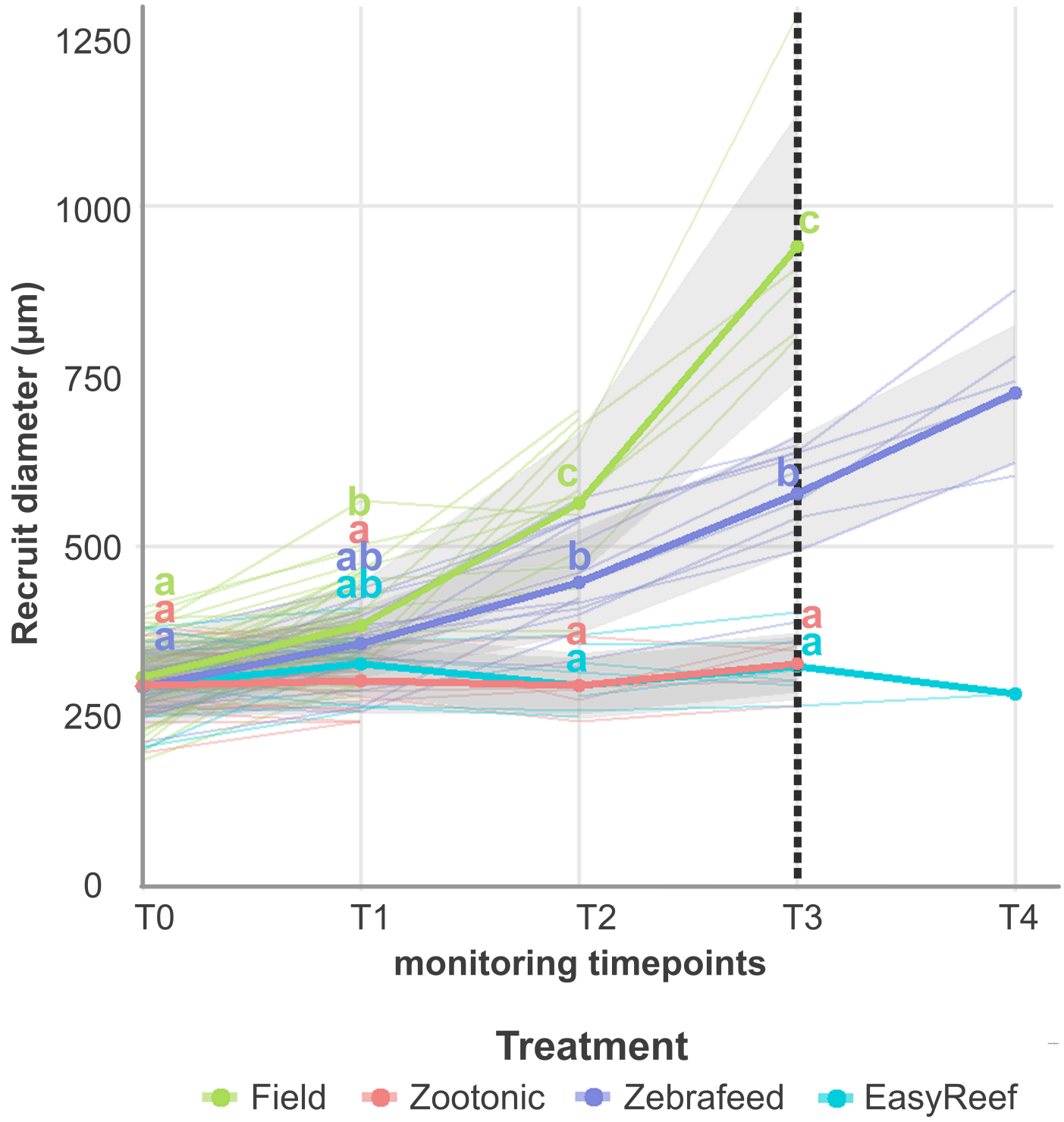


Figure 4

Figure 4 Observed growth trajectories of *Paramuricea* sp. recruits under four feeding treatments across five time points.Growth was inferred as changes in the diameter of the crown region of primary polyps (see Fig. 1). Fine lines represent individual polyps, whereas thick lines and shaded areas represent mean (±SD) size per treatment and time. Letters denote groups that are not significantly different within each time point according to post-hoc comparisons of model-estimated marginal means (Sidak-adjusted, α =

0.05, **Table S 11**). The dashed line indicates when the three *ex situ* treatments were transferred to *Zebrafeed*.

Supplementary Files

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- Feeds.xlsx
- Video1Zebrafeedfeeding.mp4
- Video2zootonic4x.mp4
- TableS1.xlsx
- TableS2.xlsx
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- TableS4.xlsx
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