

Early-stage heterotrophy and feeding effects on growth and survival of sexually produced elkhorn coral (*Acropora palmata*) spats

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Abstract

Early post-settlement stages represent a critical bottleneck in the life of sexual coral spats, yet the role of heterotrophic feeding during this period remains poorly understood. Despite its ecological importance and critically endangered status, little is known about the early heterotrophic capacity of the Caribbean elkhorn coral *Acropora palmata*. We conducted a two-week ex situ manipulative feeding experiment to assess whether heterotrophic feeding enhances growth and survival in newly settled *A. palmata* spats. The spats were produced from gametes collected on 21 August 2024 from the Southeastern Reefs Marine Sanctuary in the Dominican Republic (18°19'57"N, 68°48'46"W); the experiment began one day after metamorphosis. The spats were exposed to three feeding regimes – homogenized *Artemia* nauplii of two different stages and a commercial plankton blend – and compared to unfed controls. Feeding was associated with enhanced growth, with all three feeding treatments showing higher predicted relative growth rates than the absolute control. The strongest effect was observed for freshly hatched *Artemia*, corresponding to an approximately 8% greater increase in spat surface area over 14 days compared with the absolute control. Survival remained consistently high across treatments (> 97%), indicating that heterotrophy might be less relevant for short-term post-settlement survival. For the first time, active zooplanktivory in this species was documented as early as nine days after metamorphosis. Our results suggest that heterotrophic feeding is available to young *A. palmata* spats and could be a promising practice to improve coral restoration outcomes.

Introduction

Coral reefs are among the most biologically diverse and economically valuable ecosystems on the planet, providing habitat for approximately 25% of marine species and supporting fisheries, tourism, and coastal protection (McAllister 1995; Reaka-Kudla 1997; Moberg and Folke 1999; Brander et al. 2007; Burke et al. 2011; Spalding et al. 2017). However, these ecosystems are undergoing rapid global and local degradation due to a variety of both, natural and anthropogenic stressors (Jackson et al. 2014; Descombes et al. 2015; Eddy et al. 2021).

In the Caribbean, the reef-building elkhorn coral, *Acropora palmata* (Lamarck 1818), was once abundant and played a critical role in creating and maintaining complex reef structures (Jackson 1992; Aronson and Precht 2001; Precht and Aronson 2004). Yet, the species has suffered population reductions of > 98 %, primarily driven by disease outbreaks, hurricane disturbance, and temperature-induced bleaching events (Bruckner 2003; Jackson et al. 2014; Wicquart et al. 2025). The geographical isolation of many *A. palmata* colonies, resulting from the dramatic declines, has led to very low to non-existent natural sexual recruitment despite its relatively long pre-competency phase that allows for long-distance dispersal (Szmant 1986; Bruckner 2003; Miller et al. 2024). Local stands rely heavily on asexual reproduction via fragmentation, leading to high clonality on individual reefs (Baums et al. 2006). Recently, a Caribbean-wide genetic study found low genetic differentiation across its range (Baums et al. 2026). The consequent loss of genotypic diversity could further exacerbate its reproductive challenges (Baums et al. 2013) and ultimately affect the persistence of the species.

Even when sexual reproduction occurs, the early post-settlement stages remain a critical bottleneck in the life of coral recruits (Dela Cruz and Harrison 2020; Sarribouette et al. 2022; Edmunds 2023). High post-settlement mortality is often linked to vulnerability to predation and competition, limited energetic reserves as well as reduced photosynthetic capacities resulting from sedimentation and settlement preferences for cryptic, low light areas (Fabricius et al. 2003; Raymundo and Maypa 2004; Petersen et al. 2008; Doropoulos et al. 2012; Conlan et al. 2017). Given the challenges of natural recruitment, active coral restoration through Assisted Sexual Reproduction (ASR) has been proposed as a strategy to enhance genetic diversity and adaptability, mitigate post-settlement mortality and support the recovery of endangered coral species like the Caribbean acroporids (Chamberland et al. 2015; Miller et al. 2024).

Despite its ecological significance and critical condition, much remains unknown about the early-life ecology of *A. palmata*. Only few studies have examined its physiology, growth dynamics, and survival strategies in the first weeks post-settlement (Hirose et al. 2008; Miller 2014; Mendoza Quiroz et al. 2023). While juvenile and adult *A. palmata* are known to feed on mesozooplankton (Lewis and Price 1975), the heterotrophic behaviour of early-stage recruits is not well understood and the onset and mechanism of feeding in newly settled spats remain unknown (Geertsma et al. 2022; Schutter et al. 2023). In an ex situ setting, zooplankton capture has not been observed in *A. palmata* during the first 20 days post metamorphosis (Geertsma et al. 2022; Schutter et al. 2023). This has been attributed to different food preferences or the possibility of nematocysts only being triggered by prey items with higher kinetic energy levels (Geertsma et al. 2022). In addition, *A. palmata* might not need to develop heterotrophy early on due to its occurrence in shallow waters with high light availability (Geertsma et al. 2022). Undoubtedly, this stands in contrast to other Caribbean shallow water species such as *Orbicella faveolata* or *Diploria labyrinthiformis* which initiate zooplanktivory ex situ after no more than six days post metamorphosis (Geertsma et al. 2022). *A. palmata* develops its feeding structures (mouth and tentacles) within days after settlement (Randall et al. 2020), indicating that early heterotrophy could be available to the species.

Research on other scleractinian coral species, primarily from the genera *Acropora* and *Pocillopora*, has demonstrated that exogenous feeding can substantially promote growth and, to some extent, improve the survival of young sexual recruits (Petersen et al. 2008; Toh et al. 2014; Conlan et al. 2017; Lippens and Banaszak 2025). To our knowledge, only one study has demonstrated that feeding *A. palmata* spats produced through ex situ ASR, can enhance size and post-outplanting survival (Schutter et al. 2023), thereby helping them transition more quickly through the critical and most vulnerable post-settlement stages (Raymundo and Maypa 2004; Petersen et al. 2008). Although no capture or ingestion of brine shrimp nauplii, which were provided as food source, was observed during the 14-week aquaculture period, fed recruits were 1.2 times larger than unfed controls by the end of the experiment. This suggests that the effect of feeding was indirect (Schutter et al. 2023). Importantly, spats in the experiment were cultured with coral fragments acting as symbiont donors to facilitate early acquisition of zooxanthellae (Schutter et al. 2023). However, heterotrophic feeding might be particularly important in cases when symbionts cannot be readily acquired, due to natural causes or because of specific ex situ culture conditions. In the absence of heterotrophy, the coral would need to rely entirely on its restricted

endogenous energetic reserves (Towle et al. 2015), which would severely limit its ability to survive over extended periods.

Despite the benefits of prolonged ex situ aquaculture periods, these extended durations are not always feasible in coral restoration practice, where space, labor, infrastructure, and operational costs often constrain how long larger numbers of sexual recruits can be maintained before outplanting. It is therefore important to determine whether heterotrophic feeding can generate measurable benefits over shorter, operationally realistic timeframes. Assessing the effects of short-term feeding may help identify simple interventions that can be integrated into existing ASR and husbandry workflows without substantially increasing capacity demands.

Experiments with *A. palmata* spats have utilized brine shrimp (*Artemia*) nauplii as a food source (Geertsma et al. 2022; Schutter et al. 2023), with feeding resulting in increased spat size and improved post-outplanting survival in at least one study (Schutter et al. 2023). Freshly hatched *Artemia* nauplii therefore represent a relevant reference diet for assessing heterotrophic feeding in this species. However, identifying feeding strategies that are both biologically effective and operationally feasible requires testing alternative diets. One potential modification is the use of starved *Artemia* meta-nauplii, whose altered nutritional profile, including reduced lipid content, may influence their suitability for early coral recruits (Vanhaecke et al. 1983; Navarro et al. 1991). This is relevant because lipid-rich diets have been shown to negatively affect growth in adult acroporids (Conlan et al. 2019). In addition, commercially available plankton blends may provide a practical alternative for restoration practitioners, as they require less effort than live feeds and could be more easily integrated into existing husbandry protocols. Comparing freshly hatched *Artemia* nauplii with starved meta-nauplii and a commercial zooplankton-phytoplankton blend therefore allows us to assess whether the growth response of newly settled *A. palmata* recruits depends on prey developmental stage and nutritional condition, and whether a readily available commercial diet can offer a practical alternative to live *Artemia* for short-term ex situ husbandry.

We conducted a controlled 2-week feeding experiment to test whether feeding enhanced the growth and survival of early-stage sexual coral spats of *A. palmata*. Although this duration is shorter than in other feeding experiments, it reflected the period for which the spats could realistically be maintained in husbandry at the Dominican Foundation for Marine Study (FUNDEMAR) at the time of the experiment. The study was therefore designed to generate evidence directly applicable to refining the organization's ASR and husbandry procedures. In line with the applied objective, we tested three feeding regimes: feeding with (1) homogenized, freshly hatched *Artemia* nauplii, (2) homogenized, 1-day old starved *Artemia* meta-nauplii, (3) commercial zooplankton-phytoplankton blend.

In a parallel experiment, we monitored the feeding of *A. palmata* spats with homogenized and live *Artemia* nauplii to assess the onset of prey capture and assess whether the effect of feeding was mediated exclusively indirectly (Geertsma et al. 2022; Schutter et al. 2023).

Materials and methods

Ex situ sexual propagation and coral culture

Gamete bundles of *Acropora palmata* were harvested in situ during the spawning event of August 21, 2024 from a reef located in the Southeastern Reefs Marine Sanctuary (*Santuario Marino Arrecifes del Sureste*) in the Dominican Republic (GPS: 18°19'57 N, 68°48'46 W). The gamete bundles from 13 colonies were immediately transferred to the laboratory of FUNDEMAR for ASR ex situ, following FUNDEMAR's sexual propagation approach (Sellares-Blasco et al. 2021). A total of approximately 10,000 embryos produced during that night were distributed between three 20-liter closed-system aquaria filled with filtered sea water (FSW). The cultures were kept under static conditions and at constant temperature, controlled via air temperature. Manual cleaning from grease and dead organisms was performed on a daily basis with 50 %-water changes done every other day. Four days after fertilization, the planula larvae started to show signs of settlement competency. On Day 5 post-fertilization, 86 preconditioned ceramic disks (3.8 cm diameter x 1 cm height) were added to the aquaria as settlement substrates (hereafter referred to as seeding units, SU). Prior to the experiment, the SU had been conditioning in plastic crates adjacent to a reef for eight weeks to allow for the development of a bacterial biofilm and the availability of crustose coralline algae (CCA). Although CCA cover remained limited after the conditioning period, no fouling was observed, rendering the SU suitable for larval settlement.

Once the larvae had settled and metamorphosed into coral spats, air stones were added to the aquaria, providing constant aeration. Overall, the process resulted in an average settlement density of 17.3 ($\pm$ 10.4, n = 49) spats per SU eight days after fertilization. SU were then randomly distributed into two subsets: 49 SU were assigned to the main feeding experiment while 37 SU were kept separate to assess the onset of zooplanktivory.

Feeding experiment

The feeding experiment was initiated one day post metamorphosis (nine days after fertilization). The SU assigned to the feeding experiment were randomly transferred to 15 experimental holding tanks, each holding three to four SU placed on plastic grids (egg crates) 1 cm above the bottom. The holding tanks with their respective SU were randomly assigned to one of a total of five treatment groups: (1) feeding with homogenized, freshly hatched *Artemia* nauplii (NA); (2) feeding with homogenized, 1-day old starved *Artemia* meta-nauplii (MNA); (3) feeding with a commercial zooplankton-phytoplankton blend (CD); (4) a procedural control (PC), in which spats underwent the same handling and transfer procedures as the feeding treatments but received no food; and (5) an absolute control (AC), in which spats received no food and remained in their holding tanks throughout the experiment (Fig. 1).

The holding tanks were kept in the laboratory of FUNDEMAR at constant temperature ($29.9^{\circ}\text{C} \pm 1.1$, n = 16), controlled via air temperature, and with illumination from ceiling lights during daytime. The tanks

were of the size 16 cm × 8 cm (diameter × height), included air stones as a source of aeration and were each filled with 1 L of FSW. Daily full water changes were performed to minimize the risk of biofouling (Huang et al. 2020; Schutter et al. 2023).

Feeding of the coral spats was conducted over fourteen consecutive days in the late afternoon, representing the time of the day when the zooplankton abundance in shallow coral reefs would be highest (Heidelberg et al. 2010). During each feeding session – carried out according to the treatment conditions described in the following sections – the SU were transferred to separate feeding tanks where they were kept for two hours. Each tank contained 4 L of FSW and accommodated all SU belonging to the respective treatment. After conclusion of the feeding process, all SU were carefully rinsed with FSW and transferred back to the respective holding tank.

The procedural control (PC) allowed us to account for effects associated with handling, transfer, and cleaning procedures, whereas the absolute control (AC) accounted for conditions in the absence of both feeding and the experimental handling routine.

Artemia culture

Artemia monica (Verrill 1869) of the San Francisco Bay strain were cultured for use in the two *Artemia* feeding treatments, following a culture protocol developed in line with Lavens and Sorgeloos (1996) and Rahman and Sorgeloos (2022). The first *Artemia* culture was initiated 48 hours prior to the beginning of the experiment; a new culture was then set up on a daily basis. *Artemia* cysts were incubated for 24 hours. Afterwards unhatched cysts as well as eggshells were removed, and the hatched nauplii were rinsed with FSW. Half of the nauplii were used for feeding instantaneously after hatching (NA treatment), the other half was kept in FSW for feeding under the 1-day meta-nauplii treatment (MNA) on the consecutive day.

Feeding regimes

For both *Artemia* feeding treatments (NA, MNA), a feeding density of 20,000 individuals L⁻¹ was targeted. Most studies used prey densities of 100–10,000 individuals L⁻¹ (Hii et al. 2009; Toh et al. 2013; Hoogenboom et al. 2015; Geertsma et al. 2022). Since prey availability should not be a limiting factor in this study, a nauplii density of 20,000 individuals L⁻¹ was chosen. Densities were confirmed by taking subsamples which were analyzed under the stereo microscope.

The *Artemia* nauplii were rinsed with FSW and homogenized with 200 mL of FSW in a regular kitchen blender at low power. After 9 seconds, the feeding solution contained mostly dead *Artemia* parts of varied sizes as well as some living individuals. The homogenization of *Artemia* nauplii was performed to ensure that neither their size (~ 0.5 mm) nor their speed of movement would hinder their capture by the coral spats. Homogenized *Artemia* nauplii have previously been used successfully in planula larvae feeding experiments (Rodd et al. 2022; Rodd et al. 2025).

Under the commercial diet (CD) treatment, spat were offered a liquid natural phytoplankton blend (Easysps EVO) composed of *Tetraselmis chuii*, *Phaeodactylum tricornutum*, and *Isochrysis galbana* purchased from the supplier Easy Reefs®. A dosage of 0.125 mL of natural plankton blend per liter of water volume was applied, thus 0.5 mL per feeding tank.

Once the feeding solutions were added, the water in all feeding tanks was moderately stirred every 5–10 minutes to prevent the sinking of feeding particles and ensure water movement.

Data collection

At the beginning of the feeding experiment, each spat was identified with a unique combination of SU number, settlement side, and a consecutive spat number to allow for the tracking of survival and growth of each coral spat over time.

Spat sizes were determined on the first and last days of the experiment by photographing them next to a measurement scale through a stereo microscope. Sizes were measured with the image analysis software ImageJ (Schneider et al. 2012) by manually outlining every photographed spat and calculating its two-dimensional surface area in mm². Growth was expressed as the daily relative growth rate (RGR) in spat surface area and calculated as the difference of the natural logarithms of final and initial size, divided by the time difference in days.

The survival of coral spats was determined weekly by assessing whether the respective spat remained alive or died as compared to the initial mapping. In addition, data on several variables were recorded for use as potential covariates in the statistical analyses. The distance (in mm) to the nearest neighboring spat, measured at the beginning of the experiment, was included to account for potential growth suppression as a result of competition between spats that had settled in close proximity. Similarly, spat density, expressed as the total number of spats on the respective side of an SU, was included to account for potential density dependence. Settlement side (top or bottom) was considered relevant because prey access may have been more limited for spats located on the bottom side of an SU. Finally, initial spat size (two-dimensional surface area, mm²) was included as a potential covariate because growth and survival were expected to depend on spat size. Accounting for initial size controlled for pre-existing variation among spats, thereby reducing potential confounding in the assessment of treatment effects.

Onset of zooplanktivory

In a second experiment, we monitored the feeding behaviour of *A. palmata* spats with homogenized and living *Artemia* nauplii to visually confirm prey capture. *A. palmata* spats from 37 SU which were not part of the main experiment were observed and recorded under the stereo microscope on their feeding behavior. The SU were picked randomly on a daily basis. Spats were fed with a mixture of homogenized and alive *Artemia*, and selected spats were filmed for at least 60 minutes. In the absence of a constant

water flow rate, the water was regularly stirred. Videos were then analysed for any apparent feeding activity of the spats.

Data analysis

Mixed Model Analysis of Variance (Mixed Model ANOVA) was employed using the “lme4”- and “stats”-packages in R to assess the effect of feeding on growth. Model assumptions, including normality and homoscedasticity of residuals, independence, linearity, absence of influential outliers, and multicollinearity, were tested and found to be met.

In the case of survival, the dataset was transposed to long format, allowing for the tracking of survival across several timepoints (weekly). To assess whether there was an effect of treatment on spat survival, a binomial Generalized Linear Mixed Model (GLMM) fit by maximum likelihood (Laplace Approximation) was employed. Model diagnostics were assessed using DHARMA residual simulations, autocorrelation tests, and variance inflation factors. No evidence of overdispersion, multicollinearity, non-linearity of the logit, or systematic residual patterns was detected.

All models were analyzed using a Type III ANOVA. Covariates for initial spat size, spat density, and the distance to the nearest neighboring spat as well as random effects for SU settlement side, holding tank and SU-level variability within the holding tank were included only when a significant contribution to the models was detected. The final growth model included treatment, initial spat size, distance to the nearest neighboring spat, and the treatment × initial size interaction as fixed effects, with settlement side included as a random intercept. The final survival model included treatment and initial spat size as fixed effects, with settlement side included as a random intercept.

When coefficients were significant, post hoc pairwise comparisons using Tukey’s adjustment for multiple comparisons and simple slope analysis for interaction terms were performed using the “emmeans”-package. All statistical analyses were performed in R using RStudio (Version 4.3.2).

Results

Descriptive Statistics

At the beginning of the experiment, upon metamorphosis into coral spats, the *A. palmata* spats varied considerably in size, ranging between 0.32 to 2.21 mm². On average, initial spat size was 1.12 mm² (± 0.34 , $n = 597$; here and henceforth: mean $\pm$ standard deviation (SD)).

By the end of the experiment, the daily relative growth rate of coral spats was 0.0023 (± 0.0144 , $n = 597$). A RGR value of 0.0023 day⁻¹ indicates that spat surface area increased by approximately 0.23% day⁻¹ (calculated as $e^{0.0023} - 1$), corresponding to an estimated 3.27% increase over the 14-day experimental period. Mean growth was higher in fed spats (0.0040 ± 0.0135 , $n = 345$) than in the procedural control (0.0000 ± 0.0144 , $n = 124$) and absolute control groups (-0.0005 ± 0.0163 , $n = 128$). In all treatment

groups some spats showed negative growth, with an overall RGR range of -0.0604 to 0.0505 day^{-1} . This shrinking of spats was particularly common in the absolute control group where it affected almost half of the spats.

Survival remained high across treatments, with a mean survival rate of 98.10% (± 0.14 , $n = 844$) after the first week and 97.16% (± 0.17 , $n = 844$) at the end of the experiment. Survival was lower when spats were smaller ($< 0.8 \text{ mm}^2$) at the start of the experiment and reached 100% for spats of 1.4 mm^2 or larger (Supplementary Fig. 1).

Feeding effect on growth

Feeding treatment significantly affected growth (mixed-model ANOVA, $F_{4,592.3} = 2.46$, $P = 0.0447$; Supplementary Table 1). The strength of the treatment effect varied with initial size of the spat (Initial Size $\times$ Treatment: $F_{4,592.3} = 4.50$, $P = 0.0013$). Initial size was negatively related to RGR across treatments ($F_{1,593.3} = 137.10$, $P < 0.001$; Supplementary Table 1 and Supplementary Fig. 2), RGR was thus lower for initially larger spats. However, this negative effect was weaker in the feeding treatments than in the controls, suggesting that feeding mitigated size-dependent declines in growth rates (Supplementary Table 2).

Post hoc analyses largely supported this interpretation. Pairwise comparisons of estimated marginal means showed higher predicted RGR in all three feeding treatments compared with the absolute control (AC): (1) freshly hatched *Artemia* (NA) ($-0.00565 \pm 0.00164 \text{ SE}$, $P = 0.0056$, $|d| = 0.46$), (2) commercial diet (CD) ($-0.00455 \pm 0.00162 \text{ SE}$, $P = 0.0414$, $|d| = 0.37$) and (3) 1-day-old starved meta-nauplii (MNA) ($-0.00430 \pm 0.00166 \text{ SE}$, $P = 0.0733$, $|d| = 0.35$) (Fig. 2 and Supplementary Table 3). The standardized effect sizes were small to moderate ($|Cohen's d| = 0.35\text{--}0.46$; Supplementary Table 3), suggesting modest but relevant improvements in growth from feeding. For example, the estimated daily RGR difference of 0.00565 between the freshly hatched *Artemia* treatment and the absolute control corresponds to an approximately 8.2% greater increase in spat surface area over 14 days (calculated as $e^{0.00565 \times 14} - 1$). The strongest estimated effect was observed for freshly hatched *Artemia* nauplii, although this treatment did not differ significantly from the two other feeding regimes ($P > 0.9374$, $|d| < 0.2$, Supplementary Table 3), indicating similar growth responses to feeding.

Pairwise contrasts of treatment-specific trends confirmed significant differences between the absolute control and all three feeding treatments (AC–CD: $t_{602.1} = -3.43$, $P = 0.0059$; AC–MNA: $t_{602.2} = -3.25$, $P = 0.0107$; AC–NA: $t_{602.7} = -3.13$, $P = 0.0159$), indicating that the negative relationship between initial size and RGR was stronger in the absolute control than in the feeding treatments (Supplementary Fig. 3; Supplementary Table 4). No differences in slopes were detected among feeding regimes (all adjusted $P \geq 0.9910$).

Overall, post hoc analyses provided evidence of higher RGR in the feeding treatments relative to the absolute control, although the strength of evidence differed among feeding treatments, and none differed significantly from the procedural control.

Effect of feeding on survival rates

Feeding did not significantly influence survival (Wald $\chi^2_4 = 9.38$, $P = 0.052$; Supplementary Tables 5 and 6). Survival remained high across all treatments, with estimated survival probabilities ranging from $98.46 \pm 1.04\%$ SE in the commercial diet group (CD) to $99.65 \pm 0.28\%$ SE in the freshly hatched *Artemia* group (NA) (Supplementary Table 7). Pairwise comparisons indicated a tendency toward lower survival in CD compared with NA, with the odds of survival for spat fed with freshly hatched *Artemia* being approximately 4.5 times higher than for those fed with the commercial diet. However, this difference was not statistically significant after Tukey adjustment (odds ratio = 0.223, $z = -2.69$, $P = 0.0560$; Fig. 3 and Supplementary Table 8). Initial spat size also had a significant positive effect on survival (Wald $\chi^2_1 = 58.39$, $P < 0.001$), with larger spat showing higher survival probabilities. The survival model was based on $n = 844$ individual spat and 1,688 repeated observations.

Onset of zooplanktivory

A. palmata was observed to autonomously capture both, alive *Artemia* as well as parts of homogenized *Artemia* as early as nine days after metamorphosis. In the absence of water movement, the capture of immobile *Artemia* parts was seemingly performed through ciliary currents, making prey parts converge towards the polyp's mouth. Smaller *Artemia* parts were then fully ingested by the polyp while no subsequent regurgitation was observed during the monitoring period.

When nauplii were still alive, *A. palmata* used its nematocysts and tentacles to help paralyze and capture its prey (Fig. 4). In several cases, nauplii were observed to escape shortly after capture. When prey size was large, *A. palmata* was observed to stretch out its mesenterial filaments to supposedly feed on prey outside of the polyp with no ingestion taking place (Fig. 4).

Overall, *A. palmata* was more often observed to feed on dead *Artemia* parts than on living nauplii. It was further observed that prey capture, particularly the capture of living nauplii, seemed to be facilitated by manual mixing of the water which increased contact rates.

Discussion

The results of this study demonstrate that feeding may enhance growth in *A. palmata* spat, even during shorter ex situ rearing periods of only two weeks. Overall, the findings align with previous, longer-term studies on this and other scleractinian species emphasizing the benefits of heterotrophic feeding, particularly for enhancing early growth rates (Toh et al. 2014; Latijnhouwers et al. 2022; Schutter et al. 2023; Lippens and Banaszak 2025). Over two weeks, feeding with homogenized freshly hatched *Artemia* nauplii resulted in an 8 % greater increase in surface area compared with unfed spat in the absolute control group. Although this effect may appear moderate, even modest growth gains during early ex situ rearing could represent a critical increment toward reaching the size-escape threshold (Doropoulos et al. 2012), thus potentially influencing the spat's fate after outplanting. In previous studies, *A. palmata* spat that were of larger sizes at the time of outplanting had a higher survivorship on the reef after four

months (Schutter et al. 2023). Larger spats are generally less vulnerable to benthic algal overgrowth, sedimentation, and predation, and are more likely to successfully compete for space and light (Raymundo and Maypa 2004; Boulon 2005; Schutter et al. 2023).

Among the different feeding regimes, feeding with homogenized freshly hatched *Artemia* nauplii yielded the highest growth rate. Conversely, feeding with starved *Artemia* meta-nauplii showed a positive, albeit less pronounced, growth effect. In contrast to our expectations, the lower lipid content of starved *Artemia* meta-nauplii did not seem to benefit the coral spats. In the post hoc comparisons, no significant difference between the three feeding regimes was observed.

Because some feeding treatments differed significantly from the absolute control, whereas none differed significantly from the procedural control, the observed growth response should be interpreted cautiously as a feeding-associated effect that may not be fully separable from procedural effects, such as handling or water exchange. This underscores the importance of including procedural controls in experimental designs to distinguish the effects of the intended treatment from those of the associated handling procedures.

At the end of the experiment, survival rates had remained remarkably consistent across treatments. After two weeks, all groups exhibited survival probabilities exceeding 97%, suggesting that feeding was not essential for the immediate survival of early-stage *A. palmata* spats. This is in line with findings from longer-term studies, where feeding did not immediately influence ex-situ survival, or even decreased it (Toh et al. 2014; Schutter et al. 2023). At the same time, survival rates after outplanting the spats to the reef were found to be almost twice as high for fed spats as compared to unfed ones (Toh et al. 2014; Schutter et al. 2023), indicating that feeding, through increased spat size, could influence life outcomes later on.

The experimental duration of only two weeks chosen for this study comes with some drawbacks. Extending the experiment over several weeks or months, as in previous studies, would have allowed the effects of feeding on growth and survival to become more pronounced, thereby facilitating the detection of treatment differences and the evaluation of the relative suitability of different feeding regimes. However, prolonged ex situ rearing does not always reflect the operational capacities of coral restoration practitioners, for whom space, infrastructure, labor, and maintenance demands can limit the time that sexual recruits can realistically be kept under controlled husbandry conditions. The shorter experimental duration was therefore intentionally chosen to reflect an operationally relevant timeframe and to assess whether feeding can generate measurable benefits within the constraints of applied restoration practice.

Shrinking of spats and the role of temperature in feeding

Our data revealed that relative growth rates were higher for spats of initially smaller sizes, suggesting that those spats allocated more energy to growth, while larger spats might have diverted more resources to maintaining their size (Grinblat et al. 2023; Yu et al. 2023). In fact, our model suggests that initially larger spats were to experience a reduction in surface area by the end of the experiment. To our

knowledge, this phenomenon has not yet been observed in early-stage sexual coral spats. Mendoza Quiroz et al. (2023) documented negative growth rates during the second month of their multi-year study but attributed this to hurricane damage. Also, growth rates in that study were not related to initial sizes.

A potential explanation for the shrinking of large spats could be the elevated water temperature in our experimental holding tanks ($29.9^{\circ}\text{C} \pm 1.1$, $n = 16$), being the result of the laboratory setup, where water temperature was regulated indirectly via air conditioning. Heat exposure may have constituted a pressure for the spats and could have been particularly stressful for larger spats, whose higher metabolic demands required greater energy expenditure (Towle et al. 2015).

Feeding appeared to mitigate this negative effect, as fed spats exhibited less pronounced size-related growth depression. This suggests that feeding could buffer the physiological trade-offs faced by larger spats under stress. In a previous study, spats of *Pocillopora acuta* cultured for 30 days under two different temperature conditions showed similar tissue thickness across treatments when fed, but reduced tissue thickness under high temperature when not fed. When subsequently exposed to thermal stress fed spats had up to 33% higher survivorship compared to unfed ones (Huffmyer et al. 2021). Along the same lines, adult colonies of the Caribbean acroporid *A. cervicornis* were able to maintain growth rates under thermal stress and elevated CO_2 when fed, while growth declined in unfed corals (Towle et al. 2015). In that study, increased feeding rates were not related to symbiont density but to the elevated energetic demands caused by metabolic stress (Towle et al. 2015). Heterotrophic feeding has also been shown to influence the growth of spats facing ocean acidification (Drenkard et al. 2013), a stressor known to raise the energy costs of calcium carbonate production (Cohen and Holcomb 2009; Ries 2011).

The negative effect of large initial sizes on RGR might also be explained by the way growth was measured in this study: as the change in two-dimensional surface area. This may not capture early vertical growth which could be more relevant for larger initial sizes. Yet, during the first weeks post settlement, growth in *Acropora* species is known to be primarily horizontal, forming an expanding basal plate attached to the substrate (Babcock et al. 2003; Boulon 2005). At this stage, the coral barely protrudes and remains low and encrusting to avoid predation and algal overgrowth (Boulon 2005). Growth in height in the first two weeks following metamorphosis should thus be negligible.

Ecologically, these findings underscore the importance of heterotrophic feeding for early-stage coral spats in the face of climate-related stressors, particularly elevated water temperatures. It could be assumed that the relative importance of heterotrophy for coral spats will increase in the future as climate change progresses (Huffmyer et al. 2021). For coral restoration practitioners, our results highlight the need for optimizing rearing conditions to maximize restoration outcomes.

Early onset of zooplanktivory

This study provides novel evidence of heterotrophic feeding in *A. palmata* spats as early as nine days after metamorphosis. Although the onset is later than for other Caribbean coral species, including

Orbicella faveolata, *Diploria labyrinthiformis* or *Colpophyllia natans*, which have been observed feeding on *Artemia* no later than six days after metamorphosis (Geertsma et al. 2022), it considerably advances the earliest documented onset of feeding in *A. palmata*. Previous observations failed to detect heterotrophic feeding during the first 20 days after metamorphosis in this species (Geertsma et al. 2022).

Observations of tentacular movements and the capture and ingestion of *Artemia* nauplii and particles challenge the assumption that early-stage spats of the species rely solely on endogenous energy reserves (Geertsma et al. 2022; Schutter et al. 2023). Although nauplii were not always successfully captured, *A. palmata* spats were observed using their nematocysts to immobilize living *Artemia* prey.

The capture and feeding processes appeared to be highly influenced by both kinetic energy levels and prey size, with feeding happening through both, ingestion of food particles and external feeding through mesenterial filaments. The latter has been observed in other scleractinian coral species such as *Galaxea fascicularis* (Wijgerde et al. 2012). These findings contrast with earlier studies which reported no feeding activity in early-stage *A. palmata* spats (Geertsma et al. 2022; Schutter et al. 2023), suggesting variability in feeding onset across different experimental conditions, including prey density, water flow and temperature.

External water flow seemed to be essential for facilitating prey capture, in particular for living *Artemia* nauplii. Manual mixing during feeding sessions likely simulated natural hydrodynamic conditions, enhancing prey encounter rates and feeding efficiency. Static water conditions may restrict prey availability but could reduce stress on spats' feeding structures (Wijgerde et al. 2012; Geertsma et al. 2022).

The ability of *A. palmata* spats to capture and ingest mesozooplankton early on highlights the importance of heterotrophy as an energy source during the critical early post-settlement period.

We would like to emphasize that the coral spats in this study were maintained under ex situ conditions, without the possibility to acquire symbionts which would usually serve as an important source of energy (Bythell 1988). The onset of zooplanktivory might have been influenced by this situation in which feeding could have served as a compensatory mechanism.

Conclusion

Our study demonstrates that heterotrophic feeding can enhance the growth of ex situ reared early-stage *A. palmata* spats. While feeding had a positive effect on growth, immediate survival remained consistently high under the experimental conditions. The observation that *A. palmata* spats actively captured zooplankton as early as nine days after metamorphosis challenges existing assumptions about the onset of heterotrophy and underscores the potential importance of feeding during the earliest post-settlement stages. Our findings show that measurable growth benefits can be achieved even during a relatively short ex situ culture period. Incorporating heterotrophic feeding into early-stage husbandry protocols of *A. palmata* may therefore provide a practical means of supporting early development and improving the performance of sexually propagated corals in restoration.

Statements & Declarations

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Competing Interests

The authors have no relevant financial or non-financial interests to disclose.

Author Contributions

All authors contributed to the study conception and design. Material preparation, data collection and analysis were performed by Vanessa Hartmann. The first draft of the manuscript was written by Vanessa Hartmann and all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

Data Availability

The datasets generated and analysed during the current study are not publicly but are available from the corresponding author on reasonable request.

Ethics approval and permits

Collection of *Acropora palmata* gametes and subsequent experimental work were conducted in accordance with applicable national and institutional regulations. Gamete collection was conducted under FUNDEMAR's permit MMARN-VRCyM-00512-2024, Code VCM-00618, granted by The Ministry of Environment and Environmental Resources, Vice Ministry of Coastal Marine Resources, of the Dominican Republic.

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Figures

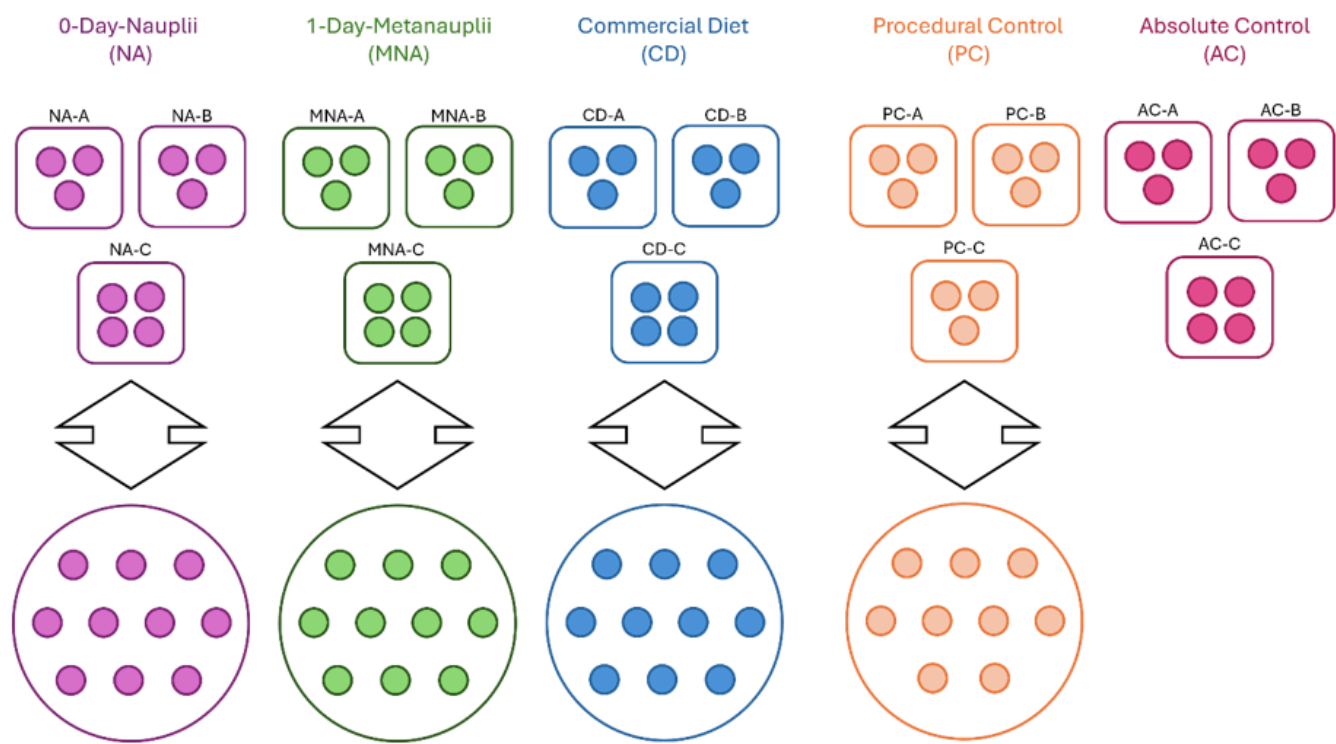


Figure 1

Visualization of the experimental setup (color-coded). Filled circles represent SU, unfilled squares represent holding tanks and unfilled circles represent feeding tanks. Purple color refers to the treatment group fed with freshly hatched *Artemia* nauplii (NA), green to the group fed with 1-day old starved *Artemia* meta-nauplii (MNA) and blue to the group fed with the commercial diet (CD). The procedural control (PC) and absolute control (AC) treatments are color-coded in orange and pink respectively. SU from the NA, MNA, CD, and PC treatments were transferred to feeding tanks on a daily basis where they remained for 2 hours before being transferred back to the holding tanks.

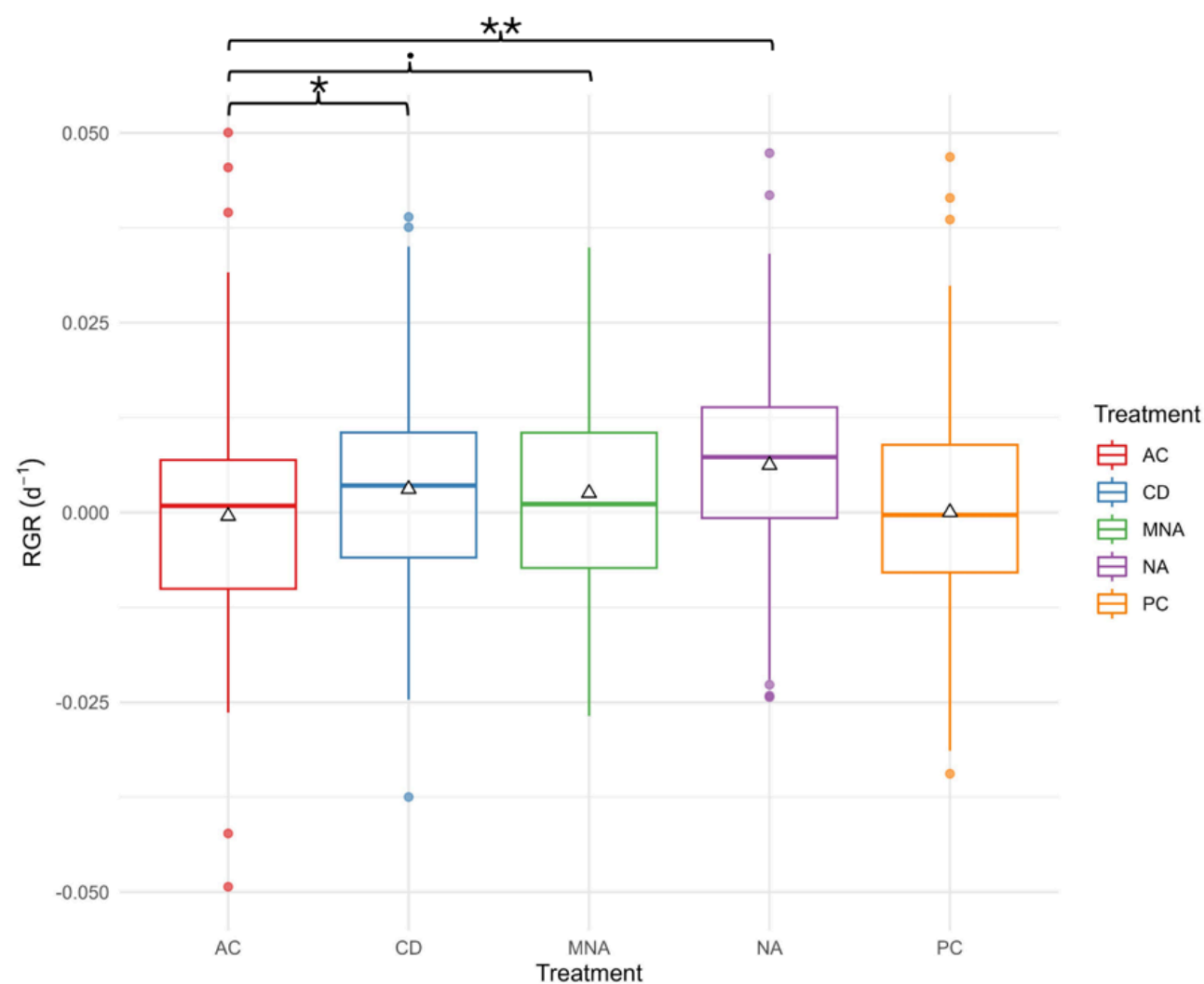


Figure 2

Boxplots of relative growth rate (RGR) (day⁻¹) by treatment group. Horizontal lines within boxes indicate medians, and open triangles indicate arithmetic means. Pairwise comparisons of estimated marginal means were performed using Tukey's adjustment. Significant group differences are shown by horizontal bars. Treatment groups: AC – Absolute Control, CD – Commercial Diet, MNA – 1-Day Meta-Nauplii, NA – Freshly Hatched Nauplii, PC – Procedural Control. Sample sizes: AC: n = 128, CD: n = 115, MNA: n = 110, NA: n = 120, PC: n = 124. Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1.

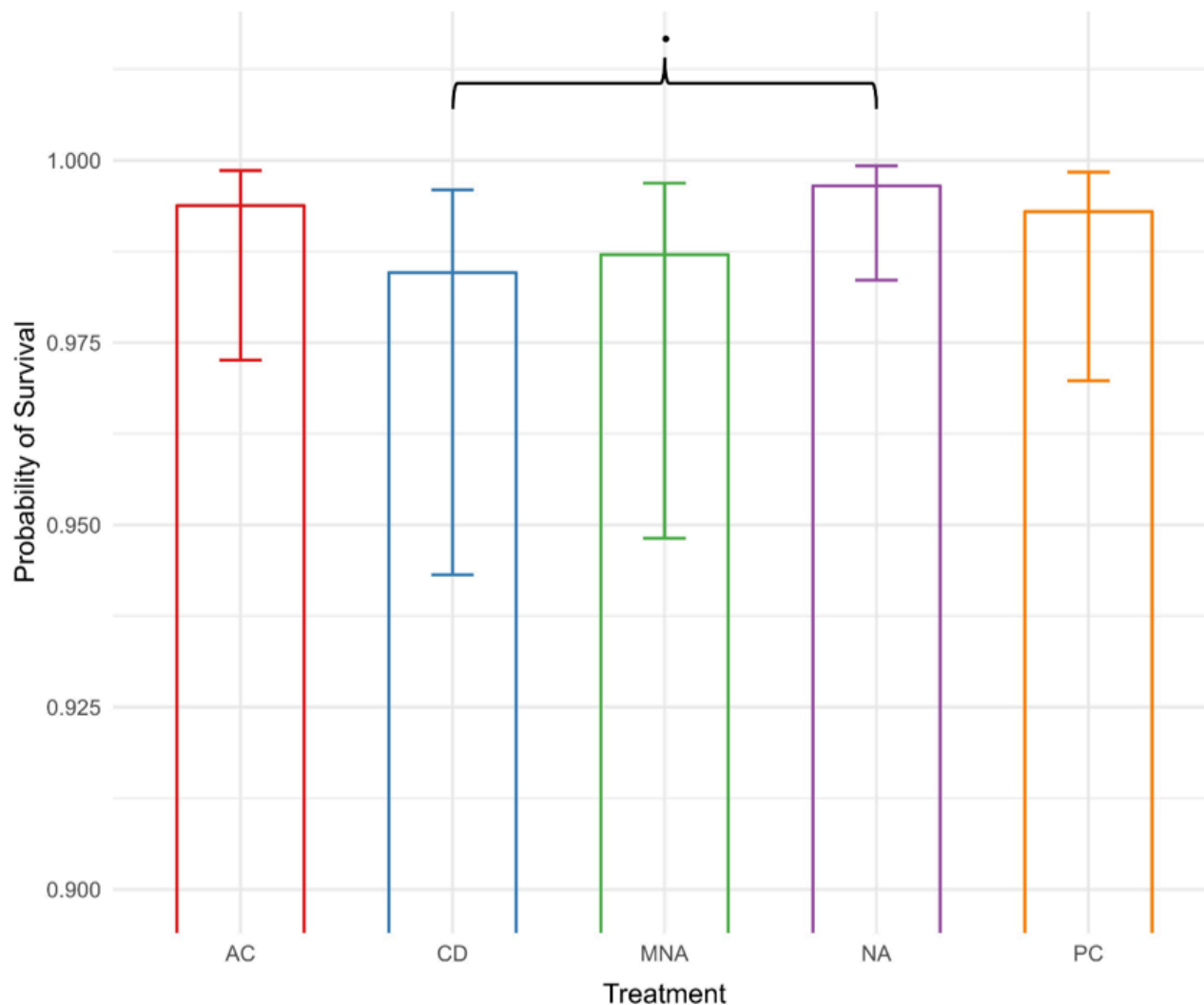


Figure 3

*Bar plots of the estimated survival probabilities by treatment group with pairwise comparisons of estimated marginal means using Tukey's adjustment. Significant group differences are shown by horizontal bars. Treatment groups: AC – Absolute Control, CD – Commercial Diet, MNA – 1-Day Meta-Nauplii, NA – Freshly Hatched Nauplii, PC – Procedural Control. The model was based on $n = 844$ individual spats and 1,688 repeated observations. Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1*

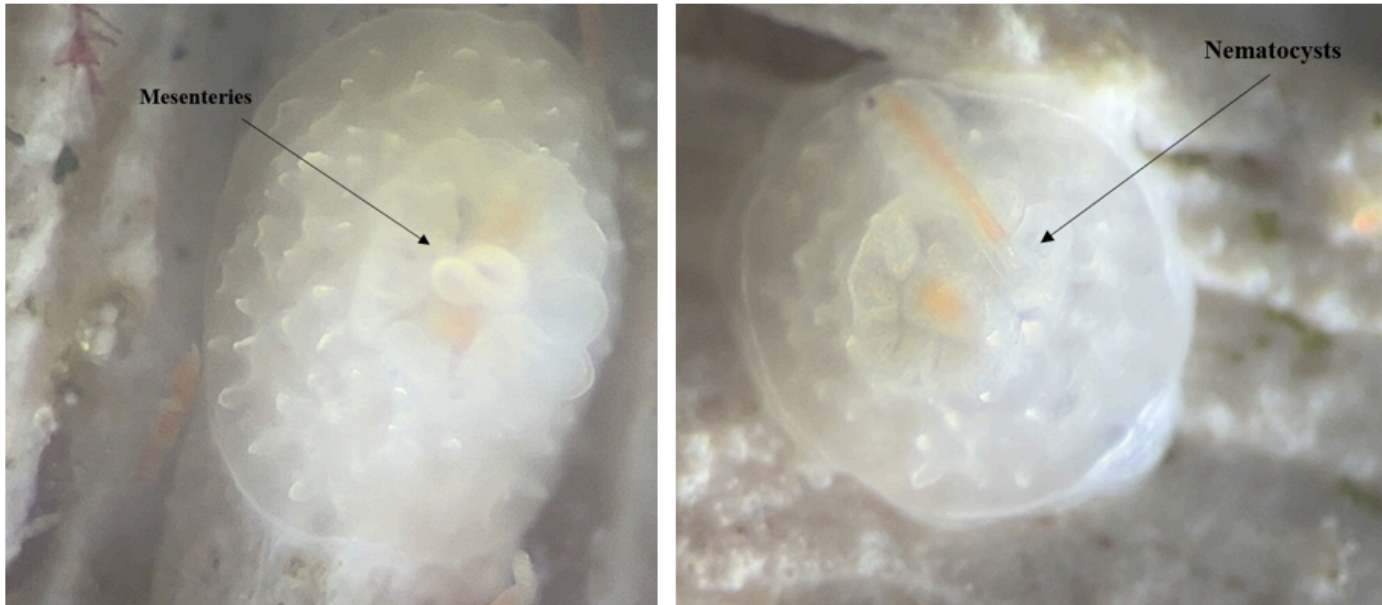


Figure 4

Pictures taken through the stereo microscope showing *A. palmata* spats (1) using their mesenteries to feed on an *Artemia* nauplius (left) and (2) ingesting an *Artemia* nauplius part while capturing a living *Artemia* nauplius with its nematocysts (right). Pictures were taken without a scale. Photographs by Vanessa Hartmann.

Supplementary Files

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