ILMU KELAUTAN: Indonesian Journal of Marine Sciences *June 2026 Vol 31(2):145-158* *e-ISSN 2406-7598*

Effects of Maternal Tissue Mortality on the Early Development of *Acropora tenuis*

Nurfaida Salam Manibpel Dumato[1,2*], Christine C. Baran[1,2], Maria Vanessa Baria-Rodriguez[1,2]

[1]Bolinao Marine Laboratory, University of the Philippines Marine Science Institute
[2]Marine Science Institute, College of Science, University of the Philippines
Velasquez Street, Diliman, Quezon City 1101, Philippines
Email: nmdumato@up.edu.ph

Abstract

As coral reefs face persistent compounded pressure from anthropogenic and environmental stressors, there is a need to assess the capacity of existing colonies on the reef to produce viable offspring. This study evaluated the impacts of maternal health, characterized by tissue mortality, on the reproductive outcomes and early development of Acropora tenuis, a vital reef-building species in the Indo-Pacific region. Specifically, this study focused on the fertilization success, larval development, larval survival, and settlement behavior of individually crossed A. tenuis colonies. In April 2024, ten colonies were collected from Caniogan Reef in the Bolinao-Anda Reef Complex, northwestern Philippines. Six colonies were categorized as healthy (0% tissue mortality) while four exhibited varying degrees of tissue mortality (10-40%). On April 27, four healthy and two unhealthy colonies spawned, resulting in three healthy and two unhealthy crosses, respectively. Results showed that Healthy crosses had higher fertilization success and normal larvae than Unhealthy crosses (Two-way ANOVA, $P < 0.05$), highlighting the influence of maternal fitness on offspring viability. Larval survival of both maternal health conditions did not vary over 10 days. Lastly, although CCA treatments initially improved settlement rates for larvae from both maternal health conditions, further analysis showed no significant differences over time, indicating that maternal health did not directly affect larval settlement during the experiment. These results underscore the vital importance of maternal health in producing viable gametes under compounded environmental and anthropogenic stresses, emphasizing the need to prioritize coral health in sexual propagation for coral culture and restoration.

Keywords: *coral health, coral reproduction, larval development, survival, settlement*

Introduction

Coral reefs are among the most biologically diverse ecosystems on earth, supporting an immense variety of marine life and providing critical ecosystem services. Not only do they contribute to biodiversity, but they also play significant roles in fisheries, tourism, and coastal protection, particularly for island and coastal communities that depend on these ecosystems for food security and economic stability (Spalding *et al*., 2017; Hoegh-Guldberg *et al*., 2019). These marine ecosystems are facing persistent threats globally due to numerous natural and anthropogenic stressors (Lu *et al*., 2018; Häder and Gao, 2023) and have faced unprecedented losses over the previous decades attributed to pollution, destructive fishing practices, mortality from bleaching, coastal development, habitat degradation, and more (Häder *et al*., 2020). If not effectively addressed, these stressors could result in irreversible damage to reef structure and function, significantly impacting both marine biodiversity and the human communities that rely on these ecosystems (Hoegh-Guldberg *et al*., 2007).

Coral reefs face both global and local threats that jeopardize their health and sustainability. Among the most pressing global stressors are ocean warming, acidification, and the increasing frequency of extreme weather events linked to climate change (Hughes *et al*., 2018). These global changes lead to widespread coral bleaching and mortality, as corals struggle to maintain symbiosis with their essential photosynthetic algae (Baker *et al*., 2008). Bleaching weakens corals, making them more vulnerable to disease and reducing their reproductive output (Baird and Marshall, 2002). On a more localized scale, reefs are affected by eutrophication, overfishing, and coastal development, which degrade water quality and increase sedimentation, further stressing coral populations (Fabricius, 2005). These combined stressors decrease coral resilience, thereby reducing their ability to recover and maintain their reproductive capabilities in the face of environmental pressures (van Oppen *et al*., 2015).

The health of coral populations directly impacts their reproductive success, structural integrity, and capacity to contribute to reef resilience.

*) Corresponding author

© Ilmu Kelautan, UNDIP

https://ejournal.undip.ac.id/index.php/ijms
DOI: 10.14710/ik.ijms.31.2.145-158

Received : 06-02-2026
Accepted : 22-05-2026

Healthy coral populations maintain higher reproductive output, enabling them to support reef recovery and replenish degraded areas (Roth *et al.*, 2018; Short *et al.*, 2025). Coral health, often assessed through factors such as tissue integrity, bleaching frequency, and disease incidence, is thus a crucial determinant of a reef's resilience and long-term viability (Baums *et al.*, 2019). This study underscores the significance of understanding coral health, especially maternal health, as a precursor to reproductive success. As corals reproduce through both asexual and sexual means, their ability to maintain viable reproductive output is essential to sustaining coral cover and promoting genetic diversity, which are vital for adapting to shifting environmental conditions (Mumby, 2009).

Coral reproductive success is influenced by various intrinsic and extrinsic factors, ranging from genetic health and tissue condition to environmental stressors (Hoegh-Guldberg *et al.*, 2019). The health of maternal coral colonies plays a particularly important role in determining reproductive output and success, influencing processes such as gamete quality, fertilization rates, and larval development (Doropoulos *et al.*, 2022). Environmental conditions like temperature and nutrient availability can further modulate these processes, often exacerbating the impact of compromised maternal health. In this context, maternal health encompasses physiological states such as tissue mortality and bleaching, which reflect a coral's overall capacity to withstand and respond to stress (Babcock and Smith, 2002). Examining how maternal health impacts reproduction, particularly in the context of persistent stressors, could reveal key insights into the reproductive strategies that underpin coral resilience.

The Bolinao-Anda Reef Complex (BARC), located in northwestern Luzon in the Philippines, represents a crucial yet vulnerable marine ecosystem that supports local biodiversity and the livelihoods of surrounding communities (Villanueva and dela Cruz, 2016; Quimpo *et al.*, 2020). This reef complex is home to a diverse array of coral species, essential for marine biodiversity and providing vital ecosystem services, including fishery resources and coastal protection (Licuanan *et al.*, 2017). Despite its ecological significance, BARC is subjected to various threats that jeopardize its health and sustainability. Key stressors include overfishing, sedimentation from terrestrial sources, and the impacts of climate change—such as ocean warming and acidification—that lead to coral bleaching and diseases (Hoegh-Guldberg *et al.*, 2019). Additionally, specific local threats like bleaching events, exacerbated by elevated sea temperatures, have caused significant coral mortality, notably in species such as *Acropora tenuis* (Briggs *et al.*, 2024). Eutrophication, driven by nutrient runoff from coastal development, further aggravates the situation by fostering algal blooms and diminishing water quality, thereby hindering coral recovery and larval recruitment (Dutra *et al.*, 2021). Research into the reproductive aspects of corals within BARC shows varied recovery and resilience; some species exhibit increased fecundity and successful larval settlement following bleaching events, indicating a potential for recovery (Villanueva *et al.*, 2012; dela Cruz and Harrison, 2020). However, the cumulative impacts of physical, chemical, and biological stressors continue to pose significant challenges to the reproductive success and long-term survival of coral populations in this area. These local stressors, in combination with global climate impacts, create a challenging environment for coral reproduction and survival, necessitating research into how maternal health may influence reproductive outcomes under such conditions.

This study addresses a critical gap in understanding how maternal health affects the reproductive output of *A. tenuis* under persisting environmental stressors. The primary research question explores the impact of maternal health, characterized by tissue mortality, on the reproductive output and early development of *A. tenuis*. This preliminary study aims to evaluate maternal health's effects on key reproductive parameters, specifically fertilization success, early larval growth and development, larval survival, and settlement behavior. By focusing on individually crossed *A. tenuis* colonies, the study seeks to identify specific areas where maternal health influences overall reproductive success, contributing to broader discussions on coral resilience and adaptation strategies.

These objectives aim to pinpoint how variations in maternal health may shape reproductive outcomes, providing insight into the resilience and sustainability of *A. tenuis* populations in the prevailing environmental stressors. By investigating the impacts of maternal health on coral reproductive outputs, this study contributes valuable data toward understanding coral adaptation and management strategies in stressed environments, especially within BARC. This knowledge is essential for developing targeted conservation and restoration strategies that strengthen coral reproductive capacity in the face of escalating environmental challenges.

Materials and Methods

The study site was located at the Bolinao-Anda Reef Complex (BARC), northwestern Philippines (16° 17' 39.1 N; 120° 00' 50.8" E) (Figure 1). BARC is one of the most extensively studied reefs in the region, and as such offers a unique opportunity to examine coral reef health and resilience. This site is particularly suitable for studying the impacts of chronic disturbances due to its exposure to various local stressors, notably eutrophication from intensive fish farming activities in the area (Villanueva and dela Cruz, 2016; Licuanan *et al*., 2017; Quimpo *et al*., 2020). These conditions make BARC an ideal natural laboratory for understanding the implications of environmental stress on coral reproductive outcomes.

Colony collection

The coral species *Acropora tenuis* was the focus of this study due to its known reproductive timing around the full moon phases of April and May at BARC (Jamodiong *et al*., 2018). Two weeks prior to the expected spawning events, a targeted sampling effort was conducted in Caniogan reef, found within BARC, to identify and collect sexually mature and gravid *A. tenuis* colonies (n=10). Colonies with intact tissue were categorized as ‘Healthy,’ while those exhibiting noticeable tissue loss or mortality were categorized as ‘Unhealthy.’ To standardize the classification of Unhealthy colonies, only corals with mortality ranging from 10-40% were selected (Meesters and Bak, 1993; Meesters and Wesseling, 1997; Cumming, 2002).

Five colonies from each health category were targeted for collection to provide a sufficient number of individually crossed broodstock for the subsequent experiments. Colonies were carefully removed from the reef using hammers and chisels and transported to the outdoor hatchery facility at the Bolinao Marine Laboratory, Marine Science Institute, University of the Philippines. The colonies were maintained in a flow-through cement tank with ample aeration until the spawning event. Mean daytime tank temperature (06:00–18:00) was 28.89±0.89 °C (range: 26.55 to 31.10 °C). The tank was partially shaded, resulting in a mean midday light intensity of 1,430 lux, with maximum values reaching approximately 13,700 lux. These conditions were intended to approximate in situ reef temperatures at the collection site. Approximately two weeks after spawning, all coral colonies were returned to their source site and cemented back onto the reef substrate.

Spawning monitoring

The colonies were isolated in individual 10 L tanks filled with UV-filtered seawater (UVFSW) at 5:00 PM each night without aeration. They were visually monitored for signs of gamete bundle setting every 30 min. Once spawning began, the colonies were allowed to release gametes for an hour before the gamete bundles were scooped from the surface with 200 mL plastic cups and transferred to their respective containers. All equipment was labeled and used exclusively for individual colonies or crosses to avoid cross-contamination (Guest *et al*., 2010; Humanes *et al*., 2021).

After 30 min, the bundles were gently agitated to release the gametes. The eggs were separated from the sperm by filtering them through a mesh filter (60 µm). The eggs were washed twice to remove any sperm residue and then transferred to their respective fertilization bowls containing 500 mL of UFSW (Humanes *et al*., 2021).

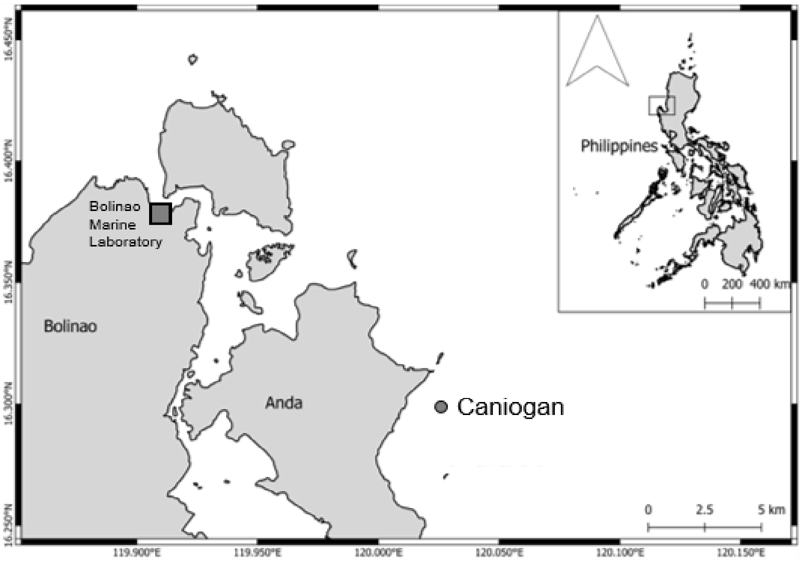

Figure 1. Map of Bolinao-Anda Reef Complex, Pangasinan, northwestern Philippines. The circle shows the colony collection site (Caniogan reef), and the square shows the Bolinao Marine Laboratory where the study was conducted.

Cross-fertilization and rearing

One of the Healthy colonies that spawned was assigned as the sperm donor (sire), while the remaining colonies were used as the mothers (dams). Sperm density was measured using a hemacytometer and diluted to approximately 900,000 sperm.mL^{-1} (dela Cruz and Harrison, 2021). Each fertilization bowl received 100 mL of the sperm solution to produce the individual crosses. After one hour, sperm washing was performed to remove excess sperm and prevent polyspermy (dela Cruz and Harrison, 2020).

Two types of crosses were produced: (1) healthy sire × healthy dam, and (2) healthy sire × unhealthy dam, hereafter referred to as 'Healthy' and 'Unhealthy' crosses, respectively. Due to spawning limitations, only healthy colonies functioned as sperm donors during the study; thus, all crosses were produced using a healthy sire paired with either a healthy or an unhealthy dam. Fertilization success for each cross was assessed 5 h post-fertilization (pf) by subsampling in 15 mL Falcon tubes (n=3). Fertilization success was quantified as the proportion of embryos exhibiting normal cleavage relative to the total number of eggs observed per subsample.

The resulting larvae from each cross were maintained in individual 5 L rearing bins at ambient temperature. To ensure optimal water quality, 50% of the water was changed daily. Mild aeration was introduced to each bin after 24 h to gently circulate the water (Guest *et al*., 2010).

Larval development

Five larvae were randomly subsampled from each cross at three timepoints (24 h, 48 h, and 72 h pf) (n=3). Larval development was assessed under a dissecting microscope (Motic SMZ-171, Hong Kong). Normal larvae were defined as those exhibiting typical morphology and motility for the species, including intact body form and active swimming behavior, following the developmental criteria described by Okubo and Motokawa (2007). Abnormal larvae were identified by irregularities in form or signs of lysis (Figure 2B). Additionally, the longest length of each larva was measured to estimate larval growth, using Motic Images Plus 3.0 software.

Larval survival

Thirty motile larvae from each cross were isolated into 300 mL containers filled with UVFSW 48 h pf (n=5). Larval survival was monitored daily for ten days. The larvae were scored as either Alive (swimming, metamorphosed, settled) or Dead (missing larvae) (Miller *et al*., 2020). Water was changed in each container every two days to maintain water quality.

Settlement behavior

A competency test was conducted three days post-fertilization to assess settlement readiness (Randall *et al*., 2024). Once competent, twenty 4-day-old larvae from each cross were isolated into containers

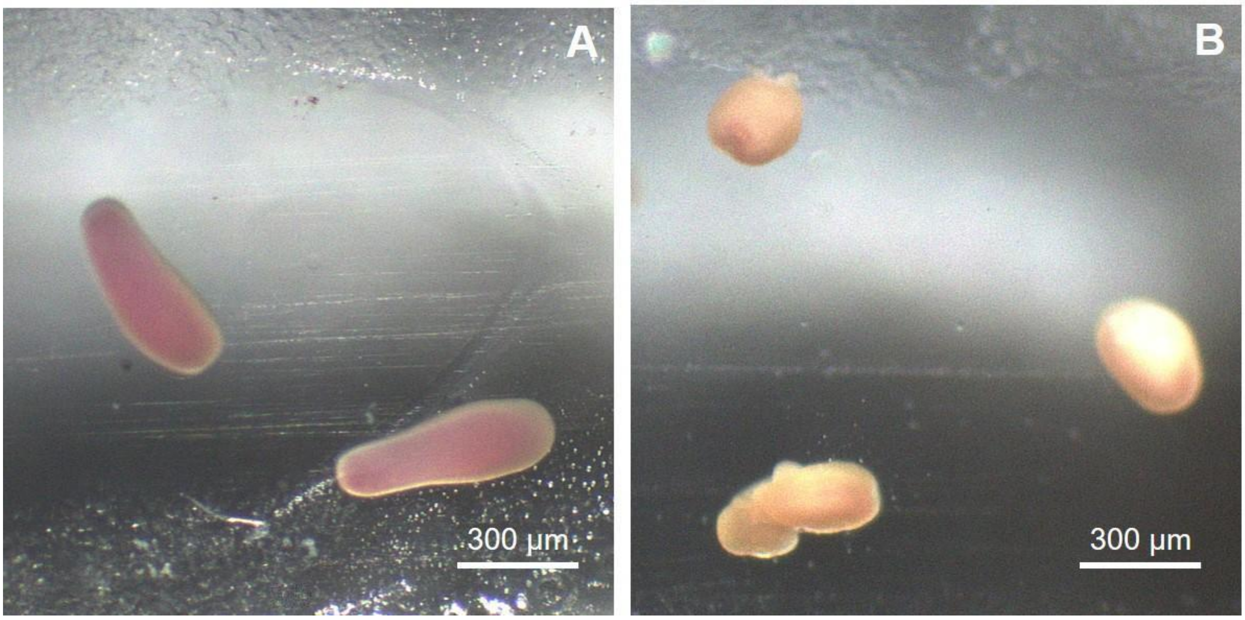

Figure 2. Representative images of four-day-old *A. tenuis* larvae exhibiting: A) normal development, and B) abnormal development.

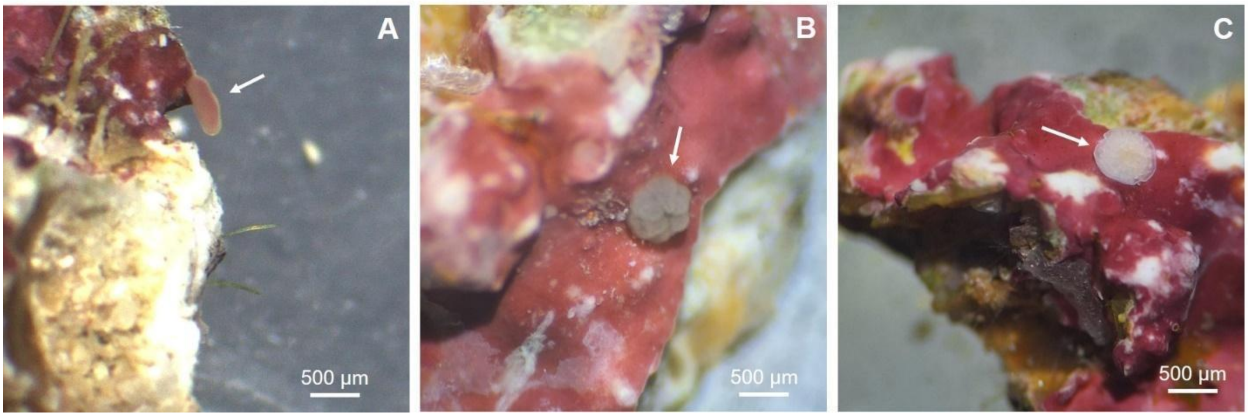

Figure 3. Representative images of settled *A. tenuis* larvae on crustose coralline algae, indicated with arrows. A) Attached, B) Metamorphosed, C) Calcified.

with and without crustose coralline algae (CCA), as the treatment and control setups, respectively (n=3). Each container was filled with 300 mL of UVFSW, and one 1 cm chip of CCA was introduced as a settlement cue in the treated setup (Lei *et al*., 2020).

The CCA chips were collected from the same reef site as the adult colonies, gently brushed to remove sediments and other attached particulates, cut into 1-cm pieces, and maintained in flow-through filtered seawater tanks prior to use in the experiment (Randall *et al*., 2024).

Larval settlement behavior was observed on Day 3 and Day 6 after the start of the experiment. Larvae were scored as Searching (swimming or crawling), Settled (attached or metamorphosed), or Dead (any missing larvae were assumed dead) (Giorgi *et al*., 2024) (Figure 3).

Data analysis

The significant differences in fertilization success, larval development, larval survival, and settlement were evaluated between healthy and unhealthy crosses. Fisher's Exact Test was employed to analyze fertilization success, a Chi-square test with Yates' correction, and Two-way ANOVA were used for larval development on data sets that were normally distributed. Kaplan-Meier survival analysis was used to visualize the larval survival of each cross type.

For settlement behavior, differences between treatments were initially assessed using a Chi-square test. To evaluate changes in settlement behavior over time, Two-way Repeated Measures ANOVA was employed, and Tukey's post-hoc comparisons were conducted to determine significant differences in the measured factors. The differences in settlement rates between crosses were compared using multiple t-tests to determine the effect of maternal health on larval settlement, and pairwise comparisons were conducted using the Holm-Šídák test to determine significance. All statistical analyses were conducted using GraphPad Prism version 8.0.0 for Windows (GraphPad Software, Boston, Massachusetts, USA, www.graphpad.com).

Result and Discussion

A total of 143 *A. tenuis* colonies were sampled in Caniogan reef, Anda, northwestern Philippines prior to the spawning event in April 2024. The total number of Healthy and Unhealthy colonies was 89 and 54, respectively. Approximately ten days before the spawning event, only six healthy and four unhealthy colonies were found to be gravid and simultaneously met the criteria for the designated 10-40% mortality established for Unhealthy corals.

While some studies reported the resilience and adaptation potential of *A. tenuis* against stressors (Hazraty-Kari *et al*., 2022), their populations in BARC were low, possibly due to recurring bleaching events and anthropogenic disturbances threatening the overall live hard coral cover since the 1980s (Cesar *et al*., 2000; Cruz-Trinidad *et al*., 2009; Cruz and Licuanan, 2011; Magdaong, 2014; dela Cruz, 2019).

Spawning and cross-fertilization

Four Healthy and two Unhealthy colonies spawned on April 27, 2024, approximately three nights after the full moon. Gamete bundle setting was first observed at 5:30 PM, and spawning commenced at 6:00 PM. The colonies were allowed to release their gamete bundles for one hour. By 7:30 PM, the gamete bundles had been scooped, and the eggs and sperm separated by 8:00 PM. Sperm counting and dilution were conducted at around 9:00 PM. The individual fertilization crosses were made at approximately 10:00 PM. The Healthy cross (healthy sire × healthy dam) had three replicates, whereas the Unhealthy cross (healthy sire × unhealthy dam) was limited to two replicates due to only two Unhealthy colonies spawning.

Aside from one Unhealthy colony that spawned on April 26, 2024, the remaining collected colonies did not spawn at all during the study period. Multiple *Acropora* species in the BARC are known to exhibit significant spawning synchronicity, particularly 6 days after the full moon (Jamodiong *et al*., 2018). Environmental factors such as sea surface temperature and wind speed significantly influence the timing of spawning events, allowing corals to adjust their reproductive strategies to maximize success (Sakai *et al*., 2020). Synchronous spawning increases the likelihood of fertilization by ensuring that compatible gametes are available at the same time, which is pertinent for corals as sessile organisms (Levitan *et al*., 2011). Deviations in this synchronicity caused by stressors could affect the reproductive output of corals and, in turn, lead to a decline in the biodiversity of coral reef ecosystems (Sorek and Levy, 2014).

Fertilization success

The mean fertilization rate in the Healthy cross was significantly higher at 85.96% compared to 69.21% in the Unhealthy cross (Fisher's exact test, $P< 0.05$) (Figure 4). This may suggest that maternal health status could influence fertilization success, potentially affecting reproductive outcomes in coral populations.

Healthy coral colonies tend to produce higher quality gametes, which can enhance fertilization success. This is partly due to the higher energetic reserves found in healthy corals, which support the production of healthier gametes resulting in more larvae per unit area produced (Hartmann *et al*., 2018). This is indicative of higher reproductive outputs for healthy coral colonies (Wada *et al*., 2014; Yoshioka *et al*., 2023). Controlled studies have also shown that cultured coral colonies typically exhibit higher fertilization rates compared to wild colonies, suggesting that optimal conditions can also significantly improve gamete quality and fertilization success (Wada *et al*., 2014).

However, coral parental health is vulnerable to environmental stressors, which can adversely affect gamete viability. Elevated nutrient levels, for instance, have been documented to decrease fertilization rates in multiple coral species (Humanes *et al*., 2017). Other factors, such as elevated sea surface temperatures and increased levels of pCO2, have been demonstrated to drastically reduce fertilization success under predicted near-future reef conditions for *A. tenuis* (Albright and Mason, 2013). This interplay of coral health and environmental conditions plays a critical role in determining the fertilization success and ultimately, the reproductive outcomes of coral populations under prevailing reef conditions.

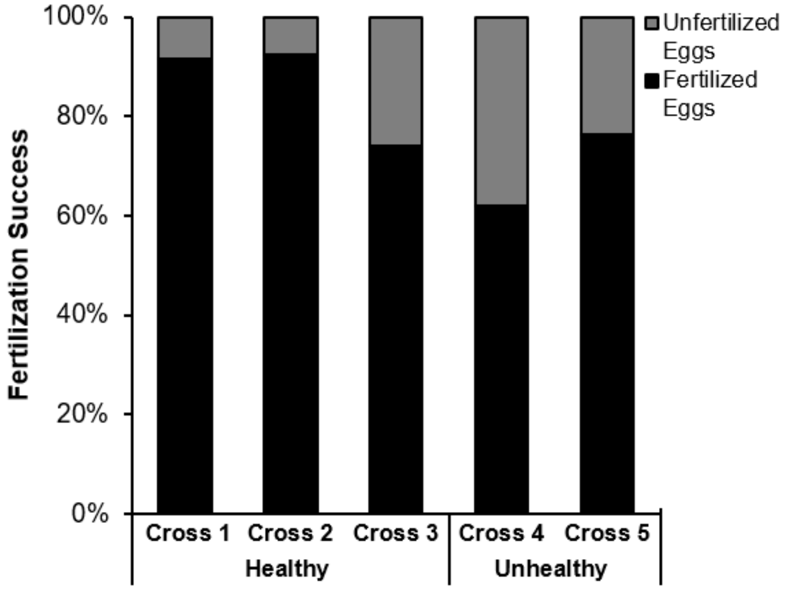

Figure 4. Proportional fertilization outcomes (fertilized vs. unfertilized eggs) for Healthy and Unhealthy crosses, with higher fertilization success observed in Healthy crosses (74-92% across three crosses) compared to Unhealthy crosses (62-76% across two crosses).

Larval development and size

There is a significant association observed between maternal health and larval development (Chi-square with Yates' correction, $P < 0.05$). The proportions of abnormal larvae were relatively higher in the Unhealthy cross than in the Healthy cross at 48 - 72 h (Figure 5A). The mean percentage for the abnormal larvae for the Healthy cross was 14.81%, whereas for the Unhealthy cross, 37.79%. These results indicate that maternal health plays a crucial role in the development of *A. tenuis* larvae. Specifically, larvae from healthy mothers exhibited a higher likelihood of normal development, while larvae from unhealthy mothers showed a significantly higher incidence of abnormalities.

There is also a significant association observed between maternal health and larval growth. Larvae from the healthy cross were on average larger by 12.59 µm (95% CI: 1.641-23.54 µm) (Figure 5B). In contrast, time did not have a discernible impact on larval size under the conditions assessed, and the combined effects of both time and maternal health also did not significantly influence larval growth ($p > 0.05$). However, a consistent trend was observed in larval size in both crosses over the three timepoints, suggesting that regardless of maternal health, the patterns of larval growth over time followed expected trajectories (Figure 5B) (Okubo and Motokawa, 2007). Larval size is commonly used as an indicator of early growth and developmental condition in broadcast-spawning corals, as larger larvae typically possess greater energetic reserves that support prolonged competency and post-settlement performance (Randall *et al.*, 2024). The observed size differences between larvae from healthy and unhealthy maternal colonies therefore suggest that maternal condition may influence early growth trajectories, even when overall patterns of size change through time remain similar across crosses (Quigley *et al.*, 2016; Chan *et al.*, 2018).

In *A. tenuis* embryogenesis, key morphological stages such as the spiral cleavage, the "prawn-chip" stage, and the bowl stage are crucial for proper larval development (Okubo and Motokawa, 2007). The similar trend in larval size observed between crosses may also be attributed to these distinct stages of embryonic and larval development, during which changes in size are noted as the larva develops cilia and begins being motile and subsequently elongates when initiating the search for a suitable substrate to settle on (Larsson *et al.*, 2014; Lin *et al.*, 2022).

Maternal health significantly influences larval development, as unhealthy mothers are likely to produce weaker and more abnormal offspring due to compromised physiological and genetic conditions. Maternal stress and health were found to directly affect the quality of gametes, leading to developmental challenges in offspring. For instance, larvae from unhealthy mothers often exhibit higher incidences of abnormalities due to the reduced viability and altered biochemical composition of the eggs, which can impair crucial early developmental processes (Lin *et al.*, 2022). Furthermore, maternal health impacts the nutritional reserves transferred to the offspring, which are essential for successful embryonic development. Poor maternal condition can result in eggs with lower lipid and protein content, reducing the energy available for critical developmental stages and increasing vulnerability to developmental anomalies (Figueiredo *et al.*, 2012). These factors collectively determine coral larval resilience and development, influencing the recruitment success critical for sustaining coral populations.

Larval survival

There was no significant difference observed in the survival of larvae from the Healthy and Unhealthy mothers ($P > 0.05$). The mean percentage of surviving larvae in the Healthy and Unhealthy crosses by Day 10 was 96.22% and 61.33%, respectively. Survival analysis revealed that larvae from Unhealthy cross exhibited a pronounced decline from Day 5 onwards, resulting in lower survival rates by Day 10 (Figure 5). These findings suggest better survival of larvae from the Healthy cross, although the differences were not statistically significant under the study conditions. This implies that factors beyond maternal health, possibly environmental or genetic, may play a critical role in larval survival (Quigley *et al.*, 2016; Chan *et al.*, 2018).

Larval survivorship is crucial for maintaining coral populations and ensuring the resilience of reef ecosystems (Adjeroud *et al.*, 2017). Factors like symbiotic relationships with algae provide supplemental energy, enhancing survival (Hazraty-Kari *et al.*, 2022). Water temperature, light availability, and salinity also play pivotal roles in larval development and viability (Baird *et al.*, 2000; Nozawa and Harrison, 2007). For example, optimal temperatures and light conditions promote growth, while extreme conditions can induce mortality (Putnam and Gates, 2015). Early acquisition of symbionts reduces mortality and improves buoyancy, crucial for successful settlement. Additionally, maternal influences significantly impact larval outcomes, with certain symbiont communities linked to higher survival rates (Quigley *et al.*, 2016; Hazraty-Kari *et al.*, 2022).

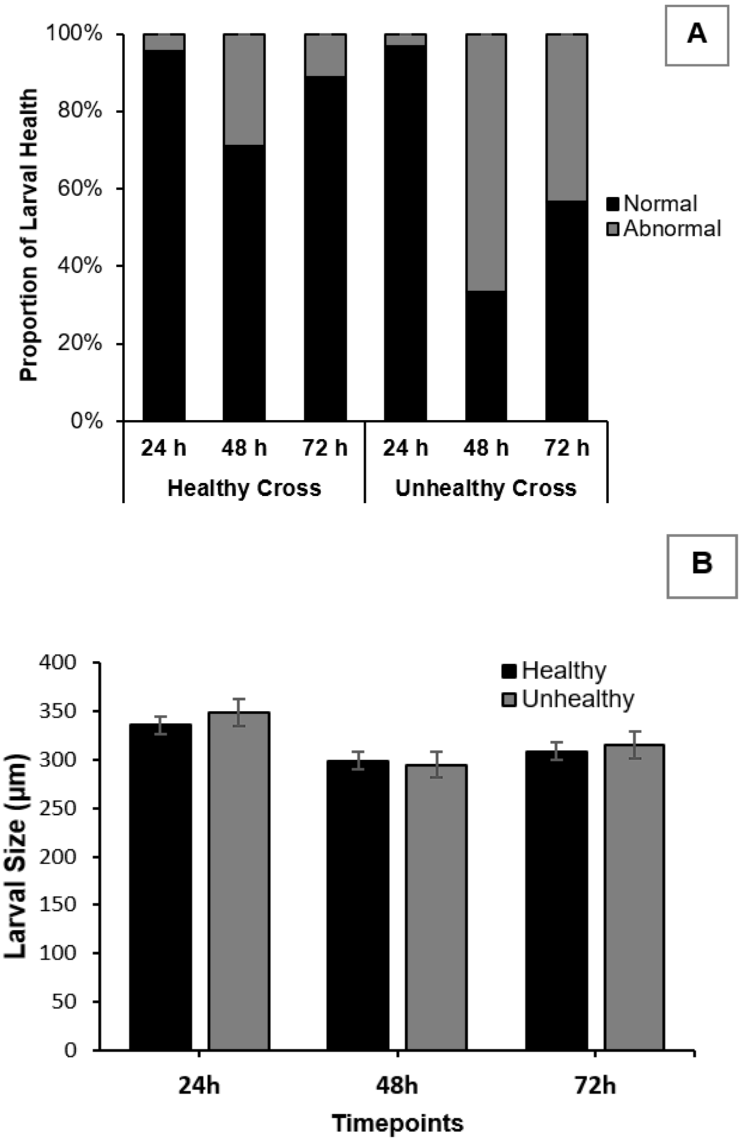

Figure 5. Larval health and size for Healthy and Unhealthy crosses. A) Proportion of larval health over time, indicating a higher occurrence of abnormal larvae in the Unhealthy cross, B) Mean size of larvae across timepoints (SE: Healthy ±8.94µm; Unhealthy ± 13.82µm).

Settlement behavior

Maternal health and the treatment conditions exhibited variable effects on the settlement behaviors of *A. tenuis* larvae. The introduction of CCA as a treatment consistently enhanced the settlement of the larvae across both Healthy and Unhealthy crosses (Chi-square, $P < 0.05$) (Figure 7). This finding aligns with the notion that CCA serves as a critical cue for larval settlement in many coral species (Lei *et al.*, 2021; Abdul Wahab *et al.*, 2023).

Analysis of larval settlement behavior over time revealed no significant differences in settlement rates between the two crosses, indicating that maternal health did not directly influence the likelihood of larvae settling over the experimental period. However, a significant interaction between treatment and time was observed, suggesting that the duration of exposure to CCA plays a pivotal role in enhancing larval settlement. Specifically, prolonged exposure to settlement cues corresponded with increased settlement rates, underscoring the importance of sustained environmental cues in coral larval behavior (dela Cruz and Harrison, 2020; Edmunds, 2023). Additionally, time might also influence settlement as the growth of the larvae continues over the duration of the experiment. This might render the larvae highly competent and ready to settle immediately, explaining the higher proportions of settled larvae by Day 6 (Figure 7) (Nozawa and Okubo, 2011; Miller *et al.*, 2020).

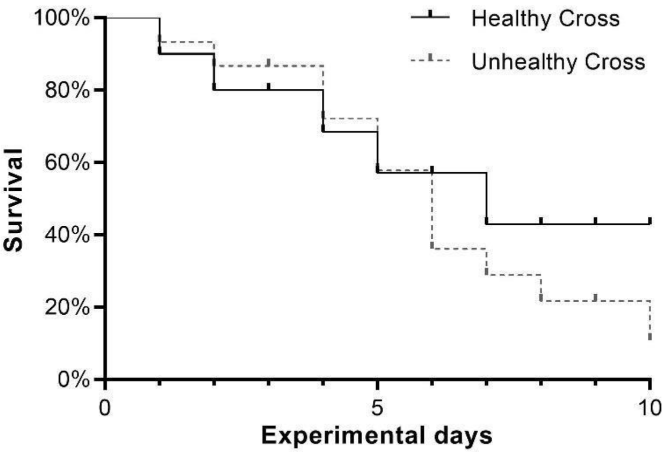

Figure 6. Percent survival of coral larvae from Healthy and Unhealthy crosses showing a decreasing trend over 10 days.

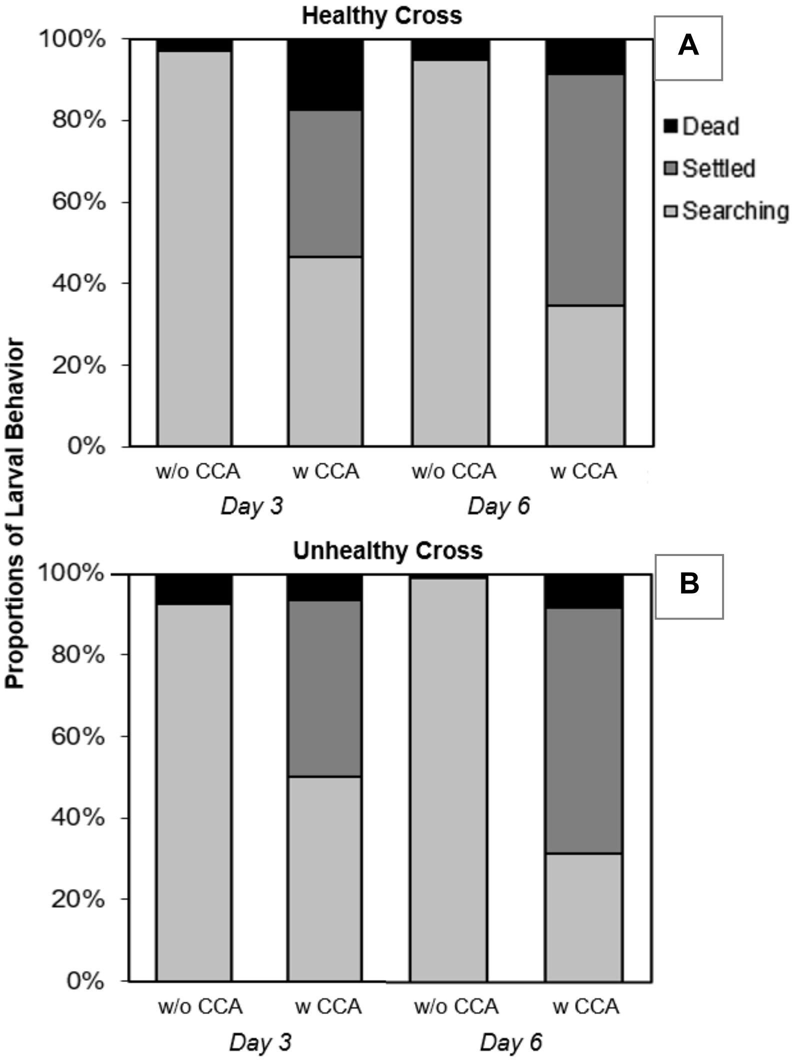

Figure 7. Larval behavior of A) Healthy, and B) Unhealthy crosses exposed with and without CCA at two time points (Day 3 and Day 6). The graph demonstrates a notable increase in the proportion of settled larvae by Day 6 under the CCA treatment.

Further analysis revealed significant behavioral differences between Healthy and Unhealthy crosses in larval behavior. In Healthy crosses, larvae exhibited significantly more searching behavior compared to settling, with an even more pronounced difference between searching and dead behaviors. However, the difference between settled and dead behaviors was not statistically significant. Conversely, in the Unhealthy crosses, although similar behavioral patterns emerged, the difference between settled and dead behaviors was now significantly different.

The results indicate that Healthy and Unhealthy crosses exhibit distinct behavioral patterns, with significant differences primarily in searching behavior. In both crosses, larvae showed a tendency to search more than they settled. The pronounced differences in the searching vs. dead comparison for both Healthy and Unhealthy crosses suggest that searching behavior is a strong indicator of larval health and vitality (Ricardo *et al*., 2017). This behavior might be driven by the necessity to avoid predation or find nutrition, which could be compromised in the Unhealthy crosses. The fact that settled versus dead comparisons were significant only in Unhealthy crosses could indicate a threshold effect where only severely impacted larvae show reduced settlement behavior, which then correlates more directly with mortality rates (Graham *et al*., 2008). These findings suggest potential applications in assessing larval health and vitality through behavioral observation. Further research could explore the underlying mechanisms driving these behavioral differences and their relationship to larval survival and developmental outcomes.

Conclusion

This study provides preliminary findings on the influence of maternal health, characterized by tissue mortality, on the spawning and early development of *A. tenuis* in the northwestern Philippines. Healthy coral colonies had higher fertilization rates and produced more normal larvae under optimal conditions compared to their unhealthy counterparts. Larval size was also significantly influenced by maternal condition, with larvae from healthy colonies being consistently larger in the first 24 h; however, growth trajectories over time remained similar. Lastly, while larval survival rates were consistent across both health conditions, larval settlement increased with the introduction of a settlement cue, yet mean settlement rates remained constant over time, indicating a varied response to different environmental factors. These results highlight the critical role of maternal health in producing viable gametes, particularly under the compounded stress of environmental and anthropogenic pressures. The results also emphasize the necessity of prioritizing coral health in the sexual mode of propagation for coral culture and restoration.

Acknowledgement

The G20 Coral Research & Development Accelerator Platform (CORDAP) funded this study under the project titled *“Quantifying and Operationalising Genetic Adaptation for Successful Coral Restoration”* (CORALADAPT), with the Gratuitous Permit No. 0396-26, led by Dr. James Guest. We are grateful to the Bolinao Marine Laboratory and the Marine Science Institute at the University of the Philippines for the use of their facilities and equipment throughout the duration of this study. We also extend our thanks to the members of the Interactions of Marine Bionts and Benthic Ecosystems Laboratory (IMBIBE) for their assistance during the fieldwork and hatchery activities. Lastly, NSMDumato wishes to express gratitude for the scholarship grant she received from the Department of Science and Technology – Science Education Institute’s Accelerated Science and Technology Human Resource Development Program (DOST-SEI ASTHRDP). This publication has been assigned Marine Science Institute Contribution No. 1628.

References

Abdul Wahab, M.A., Ferguson, S., Snekkevik, V.K., McCutchan, G., Jeong, S., Severati, A., Randall, C.J., Negri, A.P. & Diaz-Pulido, G. 2023. Hierarchical settlement behaviours of coral larvae to common coralline algae. *Sci. Rep.*, 13(1): 5795. doi: https://doi.org/10.1038/s41598-023-32676-4

Adjeroud, M., Kayal, M. & Penin, L. 2017. Importance of recruitment processes in the dynamics and resilience of coral reef assemblages. In *Marine Animal Forests*, pp. 549–569. Springer, Cham.

Albright, R. & Mason, B. 2013. Projected near-future levels of temperature and pCO_2 reduce coral fertilization success. *PLoS ONE*, 8(2): e56468. doi: 10.1371/journal.pone.0056468

Babcock, R. & Smith, L. 2002. Effects of sedimentation on coral settlement and survivorship. In *Proc. 9th Int. Coral Reef Symp.*, Bali, Indonesia, pp. 245–248.

Baird, A.H. & Babcock, R.C. 2000. Morphological differences among three species of newly settled pocilloporid coral recruits. *Coral Reefs*, 19(2): 179–183. doi: https://doi.org/10.1007/PL00006955

Baird, A.H. & Marshall, P.A. 2002. Mortality, growth and reproduction in scleractinian corals following bleaching on the Great Barrier Reef. *Mar. Ecol. Prog. Ser.*, 237: 133–141.

Baker, A.C., Glynn, P.W. & Riegl, B. 2008. Climate change and coral reef bleaching: An ecological assessment of long-term impacts, recovery trends and future outlook. *Estuar. Coast. Shelf Sci.*, 80(4): 435–471. https://doi.org/10.1016/j.ecss.2008.09.003

Baums, I.B., Baker, A.C., Davies, S.W., Grottoli, A.G., Kenkel, C.D., Kitchen, S.A., Kuffner, I.B., LaJeunesse, T.C., Matz, M.V., Miller, M.W. & Parkinson, J.E. 2019. Maximizing the adaptive potential of restored coral populations in the western Atlantic. *Ecol. Appl.*, 29(8): e01978. doi: https://doi.org/10.1002/eap.1978

Briggs, N.D., Page, C.A., Giuliano, C., Alessi, C., Hoogenboom, M., Bay, L.K. & Randall, C.J. 2024. Bleaching reduces reproductive output in *Acropora millepora*. *Coral Reefs*, 43(3): 557–569. doi: https://doi.org/10.1007/s00338-024-02483-y

Cesar, H., Pet-Soede, L., Quibilan, M.C.C., Aliño, P.M., Arceo, H.O., Bacudo, I.V. & Francisco, H. 2000. Impacts of the 1998 coral bleaching event on fisheries and tourism in the Philippines. In *Coral Bleaching: Causes, Consequences and Response*, p. 41.

Chan, W.Y., Peplow, L.M., Menéndez, P., Hoffmann, A.A. & Van Oppen, M.J.H. 2018. Interspecific Hybridization May Provide Novel Opportunities for Coral Reef Restoration. *Front. Mar. Sci.*, 5: 160. doi: https://doi.org/10.3389/fmars.2018.00160

Cumming, R.L. 2002. Tissue injury predicts colony decline in reef-building corals. *Mar. Ecol. Prog. Ser.*, 242: 131–141.

Dela Cruz, D.W. & Harrison, P.L. 2020. Enhancing coral recruitment through assisted mass settlement of cultured coral larvae. *PLoS ONE*, 15(11): e0242847. doi: 10.1371/journal.pone.0242847

Dela Cruz, D.W. 2019. Coral Reef Restoration Using Mass Coral Larval Enhancement. Ph.D. Thesis, Southern Cross University.

Doropoulos, C., Gómez-Lemos, L.A., Salee, K., McLaughlin, M.J., Tebben, J., Van Koningsveld, M., Feng, M. & Babcock, R.C. 2022. Limitations to coral recovery along an environmental stress gradient. *Ecol. Appl.*, 32(3): e2558. doi: https://doi.org/10.1002/eap.2558

Dutra, L.X., Haywood, M.D., Singh, S., Ferreira, M., Johnson, J.E., Veitayaki, J., Kininmonth, S., Morris, C.W. & Piovano, S. 2021. Synergies between local and climate-driven impacts on coral reefs. *Mar. Pollut. Bull.*, 164: 111922. https://doi.org/10.1016/j.marpolbul.2021.111922

Edmunds, P.J. 2023. Coral recruitment: Patterns and processes. *Biol. Rev.*, 98(6): 1862–1886. https://doi.org/10.1111/brv.12965

Edmunds, P.J. 2024. Why keep monitoring coral reefs? *BioScience*, 74(8): 552–560. doi: https://doi.org/10.1093/biosci/biae046

Fabricius, K.E. 2005. Effects of terrestrial runoff on the ecology of corals and coral reefs: review and synthesis. *Mar. Pollut. Bull.*, 50(2): 125–146. doi: 10.1016/j.marpolbul.2004.11.028

Figueiredo, J., Baird, A.H., Cohen, M.F., Flot, J.F., Kamiki, T., Meziane, T., Tsuchiya, M. & Yamasaki, H. 2012. Ontogenetic changes in lipid composition of coral larvae. *Coral Reefs*, 31(2): 613–619.

Giorgi, A., Monti, M., Paul, V.J., Sneed, J.M. & Olson, J.B. 2024. Larvae from three Caribbean corals settle differently in response to crustose coralline algae and their bacterial communities. *Mar. Ecol. Prog. Ser.*, 751: 53–69. doi: https://doi.org/10.3354/meps14739

Graham, E.M., Baird, A.H. & Connolly, S.R. 2008. Survival dynamics of scleractinian coral larvae and implications for dispersal. Coral Reefs 27: 529–539. https://doi.org/10.1007/s00338-008-0361-z

Guest, J.R., Baird, A.H., Maynard, J.A., Muttaqin, E., Edwards, A.J., Campbell, S.J., Yewdall, K., Affendi, Y.A. & Chou, L.M. 2012 Contrasting patterns of coral bleaching susceptibility in 2010 suggest an adaptive response to thermal stress. *PLoS ONE*, 7(3): e33353. doi: 10.1371/journal.pone.0033353

Häder, D.P. & Gao, K. 2023. Aquatic productivity under multiple stressors. *Water*, 15(4): 817. https://doi.org/10.3390/w15040817

Häder, D.P., Banaszak, A.T., Villafañe, V.E., Narvarte, M.A., González, R.A. & Helbling, E.W. 2020. Anthropogenic pollution of aquatic ecosystems. *Sci. Total Environ.*, 713: 136586.

Harrison, P.L., Dela Cruz, D.W., Cameron, K.A. & Cabaitan, P.C. 2021. Increased Coral Larval Supply Enhances Recruitment for Coral and Fish Habitat Restoration. *Front. Mar. Sci.*, 8: 750210. https://doi.org/10.3389/fmars.2021.750210

Hartmann, A.C., Marhaver, K.L. & Vermeij, M.J.A. 2018. Corals in Healthy Populations Produce More Larvae Per Unit Cover. *Conserv. Lett.*, 11(3): e12410. https://doi.org/10.1111/conl.12410

Hazraty-Kari, S., Tavakoli-Kolour, P., Kitanobo, S., Nakamura, T. & Morita, M. 2022. Adaptations by the coral Acropora tenuis confer resilience to future thermal stress. *Commun. Biol.*, 5(1): 1371. https://doi.org/10.1038/s42003-022-04309-5

Hoegh-Guldberg, O., Mumby, P.J., Hooten, A.J., Steneck, R.S., Greenfield, P., Gomez, E., Harvell, C.D., Sale, P.F., Edwards, A.J., Caldeira, K. & Knowlton, N. 2007. Coral reefs under rapid climate change. *Science*, 318(5857): 1737–1742.

Hoegh-Guldberg, O., Pendleton, L. & Kaup, A. 2019. People and the changing nature of coral reefs. *Reg. Stud. Mar. Sci.*, 30: 100699. doi: 10.1016/j.rsma.2019.100699

Hughes, T. P., Anderson, K. D., Connolly, S. R., Heron, S. F., Kerry, J. T., Lough, J. M., Baird, A. H., Baum, J. K., Berumen, M. L., Bridge, T. C. L. & Claar, D. C. 2018. Spatial and temporal patterns of mass bleaching of corals in the Anthropocene. *Science*, 359(6371): 80–83. doi: 10.1126/science.aan8048

Humanes, A., Fink, A., Willis, B.L., Fabricius, K.E., de Beer, D. & Negri, A.P. 2017. Effects of suspended sediments and nutrient enrichment on juvenile corals. *Mar. Pollut. Bull.*, 125(1–2): 166–175. https://doi.org/10.1016/j.marpolbul.20 17.08.014

Humanes, A., Lachs, L., Beauchamp, E.A., Bythell, J.C., Edwards, A.J., Golbuu, Y., Martinez, H.M., Palmowski, P., Treumann, A., van der Steeg, E. & van Hooidonk, R. 2022. Within-population variability in coral heat tolerance indicates climate adaptation potential. *Proc. R. Soc. B, 289(1981):* 20220872. https://doi.org/10.1098/rspb.2022.0872

Jamodiong, E.A., Maboloc, E.A., Villanueva, R.D. & Cabaitan, P.C. 2018. Gametogenesis and inter-annual variability in the spawning pattern of *Acropora hyacinthus* in northwestern Philippines. *Zool. Stud.,* 57: e46. https://doi.org/10.6620/ZS.2018.57-46

Larsson, A.I., Järnegren, J., Strömberg, S.M., Dahl, M.P., Lundälv, T. & Brooke, S. 2014. Embryogenesis and larval biology of the cold-water coral *Lophelia pertusa*. *PLoS One,* 9(7): e102222. https://doi.org/10.1371/journal.pone.0102222

Lei, X., Jiang, L., Zhang, Y., Sun, Y., Zhou, G., Lian, J. & Huang, H. 2021. Coral larval settlement and post-settlement survival facilitated by crustose coralline algae with or without living tissue. *Mar. Biol.,* 168(8): 128. https://doi.org/10.1007/s00227-021-03908-6

Levitan, D.R., Boudreau, W., Jara, J. & Knowlton, N. 2014. Long-term reduced spawning in Orbicella coral species due to temperature stress. *Mar. Ecol. Prog. Ser.,* 515: 1–10. https://doi.org/10.3354/meps11053

Licuanan, A.M., Reyes, M.Z., Luzon, K.S., Chan, M.A.A. & Licuanan, W.Y. 2017. Initial findings of the nationwide assessment of Philippine coral reefs. *Philipp. J. Sci.,* 146(2): 177–185.

Lin, C., Kang, C.M., Huang, C.Y., Li, H.H. & Tsai, S. 2022. Study on the development and growth of coral larvae. *Appl. Sci.,* 12(10): 5255. https://doi.org/10.3390/app12105255

Lu, Y., Yuan, J., Lu, X., Su, C., Zhang, Y., Wang, C., Cao, X., Li, Q., Su, J., Ittekkot, V. & Garbutt, R.A. 2018. Major threats of pollution and climate change to global coastal ecosystems and enhanced management for sustainability. *Environ. Pollut.,* 239: 670–680. https://doi.org/10.1016/j.envpol.2018.04.016

Magdaong, E.T. 2014. Long-term trends of coral cover in the Philippines: Trajectory, spatiotemporal patterns, and the efficacy of marine protected areas. Disertasi Doktor, Hokkaido University.

Meesters, E.H. & Bak, R.P.M. 1993. Effects of coral bleaching on tissue regeneration potential and colony survival. *Mar. Ecol. Prog. Ser.,* 96: 189–198. https://doi.org/10.3354/meps096189

Meesters, E.H., Wesseling, I. & Bak, R.P.M. 1997. Coral colony tissue damage in six species of reef-building corals: Partial mortality in relation with depth and surface area. *Mar. Ecol. Prog. Ser.,* 154: 153–161. https://doi.org/10.3354/meps154153

Miller, M.W., Bright, A.J., Pausch, R.E. & Williams, D.E. 2020. Larval longevity and competency patterns of Caribbean reef-building corals. *PeerJ,* 8: e9705. https://doi.org/10.7717/ peerj.9705

Mumby, P.J. 2009. Phase shifts and the stability of macroalgal communities on Caribbean coral reefs. *Coral Reefs,* 28(3): 761–773. https://doi.org/10.1007/s00338-009-0509-6

Nozawa, Y. & Harrison, P.L. 2008. Temporal patterns of larval settlement and survivorship of two broadcast-spawning acroporid corals. *Mar. Biol.,* 155(3): 347–351. https://doi.org/10.1007/s00227-008-1034-1

Nozawa, Y. & Okubo, N. 2011. Survival dynamics of reef coral larvae with special consideration of larval size and the genus Acropora. *Biol. Bull.,* 220(1): 15–22. https://doi.org/10.1086/BBLv220n1p15

Okubo, N. & Motokawa, T. 2007. Embryogenesis in the reef-building coral *Acropora* spp. *Zool. Sci.,* 24(12): 1169–1177. https://doi.org/10.2108/zsj.24.1169

Putnam, H.M. & Gates, R.D. 2015. Preconditioning in the reef-building coral *Pocillopora damicornis* and the potential for trans-generational acclimatization in coral larvae under future climate change conditions. *J. Exp. Biol.,* 218(15): 2365–2372. https://doi.org/10.1242/jeb.123 018

Quigley, K.M., Willis, B.L. & Bay, L.K. 2016. Maternal effects and Symbiodinium community composition drive differential patterns in juvenile survival in the coral *Acropora tenuis*. *R. Soc. Open Sci.,* 3(10): 160471. https://doi.org/10.1098/rsos.160471

Quimpo, T.J.R., Requilme, J.N.C., Gomez, E.J., Sayco, S.L.G., Tolentino, M.P.S. & Cabaitan, P.C. 2020. Low coral bleaching prevalence at the Bolinao–Anda Reef Complex, northwestern Philippines during the 2016 thermal stress event. *Mar. Pollut. Bull.,* 160: 111567. https://doi.org/10.1016/j.marpolbul.2020.111567

Randall, C.J., Giuliano, C., Stephenson, B., Whitman, T.N., Page, C.A., Treml, E.A., Logan, M. & Negri, A.P. 2024. Larval precompetency and settlement behaviour in 25 Indo-Pacific coral species. *Commun. Biol.,* 7(1): 142. https://doi.org/10.1038/s42003-024-05711-9

Ricardo, G.F., Jones, R.J., Nordborg, M. & Negri, A.P. 2017. Settlement patterns of the coral *Acropora millepora* on sediment-laden surfaces. *Sci. Total Environ.,* 609: 277–288. https://doi.org/10.1016/j.scitotenv.2017.07.153

Roth, F., Saalmann, F., Thomson, T., Coker, D.J., Villalobos, R., Jones, B.H., Wild, C. & Carvalho, S. 2018. Coral reef degradation affects the potential for reef recovery after disturbance. *Mar. Environ. Res.,* 142: 48–58. https://doi.org/10.1016/j.marenvres.2018.09.022

Sakai, Y., Kato, K., Koyama, H., Kuba, A., Takahashi, H., Fujimori, T., Hatta, M., Negri, A.P., Baird, A.H. & Ueno, N. 2020. A step-down photophobic response in coral larvae: Implications for the light-dependent distribution of the common reef coral, *Acropora tenuis*. *Sci. Rep.,* 10(1): 17680. https://doi.org/10.1038/s41598-020-747 11-2

Short, M.L., Close, H.G., Gilliam, D.S. & Figueiredo, J. 2025. A reproductive and trophic analysis of corals in a degraded environment. *Coral Reefs,* 44: 1–16.

Sorek, M. & Levy, O. 2014. Coral spawning behavior and timing. In Annual, lunar, and tidal clocks: Patterns and mechanisms of nature's enigmatic rhythms, 81–97. Springer, Tokyo. https://doi.org/10.1007/978-4-431-55261-1_6

Spalding, M., Burke, L., Wood, S.A., Ashpole, J., Hutchison, J. & Zu Ermgassen, P. 2017. Mapping the global value and distribution of coral reef tourism. *Mar. Policy,* 82: 104–113. https://doi.org/10.1016/j.marpol.2017.05.023

van Oppen, M.J.H., Oliver, J.K., Putnam, H.M. & Gates, R.D. 2015. Building coral reef resilience through assisted evolution. *Proc. Natl. Acad. Sci. U.S.A.,* 112(8): 2307–2313. https://doi.org/10. 1073/pnas.1422301112

Villanueva, R. & dela Cruz, D., 2016. Coral Reef Restoration using Mass Coral Larval Reseeding. Final report. ACIAR Canberra ACT 2601 Australia. 60 pp.

Villanueva, R.D., Baria, M.V.B. & dela Cruz, D.W. 2012. Growth and survivorship of juvenile corals outplanted to degraded reef areas in Bolinao–Anda Reef Complex, Philippines. *Mar. Biol. Res.,* 8(9): 877–884. https://doi.org/10.1080/17451000.2012.695262

Wada, N., Omori, M. & Ohdera, A. 2014. How many donor colonies should be cross-fertilized for nursery farming of sexually propagated corals? *Nat. Resour.,* 5: 521-526

Yoshioka, Y., Chiu, Y.L., Uchida, T., Yamashita, H., Suzuki, G. & Shinzato, C. 2023. Genes possibly related to symbiosis in early life stages of *Acropora tenuis* inoculated with *Symbiodinium microadriaticum*. *Commun. Biol.,* 6(1): 1027. https://doi.org/10.1038/s42003-023-05328-8