

High Local Variability in Hard Coral Juveniles Reveals Uneven Recovery Potential Across Proximate Islands in Karimunjawa, Indonesia

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Abstract

Coral reefs are vital marine ecosystems in the Karimunjawa Archipelago, Indonesia, but they face increasing threats from climate change and local anthropogenic stressors. Coral juveniles are widely recognized as reliable indicators of recent recruitment and reef recovery potential. In 2023, hard coral (scleractinian) juveniles (<10 cm in diameter) and benthic assemblages were surveyed at nine islands in this archipelago. At each island, 50 photo quadrats (50 × 50 cm), placed at 1 m intervals along a 50 m transect at a depth of ~ 7 m, were analyzed. The statistical approach zero-inflated Generalized Linear Mixed Model (GLMM) with AIC model selection was used to determine the factors influencing the abundance of hard coral juveniles. The highest coral juvenile density is on Sambangan Island (145 juveniles; 11.6 colonies.m⁻²), and the lowest is on Tengah Island (19 juveniles; 1.5 colonies.m⁻²). Most juveniles belonged to *Montipora* (49%), *Fungia* (20%), and *Porites* (6%). Hard corals dominated the benthic cover, with median island-level values ranging from 25% to 79%. Juvenile densities varied greatly among islands, with a significant positive correlation between juvenile density and hard coral cover detected at only two islands. Overall, juvenile density declined with proximity to the main Karimunjawa Island, the center of human activity. Our findings revealed unexpectedly high spatial variation in coral juvenile abundance among proximate islands, indicating differences in recovery potential and anthropogenic pressure. Our results highlight the need for island-specific coral reef conservation strategies, even across short spatial scales.

Keywords: Coral juveniles, Recruitment, Karimunjawa, Hard coral cover, Anthropogenic stressors, Conservation

Introduction

Coral reefs are vital marine ecosystems that provide economic, social, and ecological benefits to coastal communities (Bellwood *et al.*, 2019; Wijaya *et al.*, 2025). However, their survival is increasingly threatened by human activities, including overexploitation, sedimentation, nutrient enrichment, and chemical pollution (Richmond, 1993; Dachs and Méjanelle, 2010).

The Karimunjawa Archipelago, one of the few coral reef ecosystems in the Java Sea, Indonesia, consists of 27 islands spread across approximately 50 km and is located 94 km off the northern coast of Central Java. This protected conservation area is well known for its rich biodiversity and potential as a center for marine ecotourism (Fafurida *et al.*, 2020; Magfiroh and Fahrudin, 2020). Despite their ecological and socioeconomic importance, the reefs of the Karimunjawa Archipelago are under increasing

pressure. Research conducted on Karimunjawa stated that tourism activity, such as snorkeling, can increase total solid suspension (TSS) and lead to high sedimentation, which causes death to the live corals (Purnomo *et al.*, 2022). Although Karimunjawa was exposed to several warming periods from 2014 - 2018, the 2016 coral bleaching event created a huge loss to the coral cover (Kennedy *et al.*, 2020). Coral cover has been declining, with tourism identified as one of the contributing factors (Pribadi *et al.*, 2020). Sedimentation poses another major threat as it introduces both natural and pollutant particles into seawater, while the Karimunjawa Islands have several anthropogenic activities, such as tropical plantations, agriculture, settlements, and fishing, that indeed have an impact on the water quality (Dachs and Méjanelle, 2010; Halim *et al.*, 2022). Collectively, these stressors compromise coral reef health and reduce the ecological resilience of the ecosystem, thereby exerting a broader impact on the surrounding marine environment. Consequently, conserving coral

reefs in the Karimunjawa Archipelago is critical for mitigating the impact of anthropogenic stressors. These stressors, including increased sedimentation, nutrient enrichment, and pollutant inputs, degrade settlement substrate and raise post-settlement mortality, thereby reducing larval settlement rates and juvenile survival. Therefore, juvenile coral assemblages provide a direct, site-specific indicator of recent recruitment and reef resilience.

Juvenile coral assemblages, which reflect recent recruitment processes and habitat conditions, serve as valuable indicators of coral reef health and resilience. Therefore, this study aims to understand the recovery potential of coral assemblages through examining the dynamics of coral juvenile assemblages across the islands of Karimunjawa and statistically calculating the benthic categories as influencers. To examine these dynamics, hard coral (scleractinian) juvenile densities and the cover of associated benthic communities were surveyed across nine

islands in the Karimunjawa Archipelago in 2023. Our findings revealed an unexpectedly high variation in coral juvenile abundance among adjacent islands, underscoring the need for island-specific conservation strategies within the archipelago.

Materials and Methods

Study site and data acquisition

This study was conducted on nine islands in the Karimunjawa Archipelago in September 2023 (Figure 1 and Table 1). Data was collected using SCUBA diving. At each island, a 50 m line was placed along the reef slope at a depth of approximately 7 m for a single repetition. A total of 50 photo quadrats (50 cm × 50 cm) were placed at 1 m intervals along the line. Photographs of the quadrats were taken using a digital camera (Olympus Tough TG-5 or TG-6), resulting in a dataset of 50 quadrat images per island (Giyanto, 2013).

Table 1. GPS coordinates of study sites at nine islands in the Karimunjawa Archipelago, Indonesia

Islands	Coordinates	
Sambangan	S 05 ° 50'28.2"	E 110 ° 34'55.2"
Sintok	S 05 ° 46'48.5"	E 110 ° 30'27.1"
Tengah	S 05 ° 48'37.6"	E 110 ° 30'30.3"
Cemara Besar	S 05 ° 48'18.6"	E 110 ° 22'09.7"
Cemara Kecil	S 05 ° 49'50.9"	E 110 ° 22'33.2"
Menjangan Kecil	S 05 ° 53'02.9"	E 110 ° 24'33.9"
Menjangan Besar	S 05 ° 52'30.4"	E 110 ° 25'14.4"
Geleang	S 05 ° 52'30.6"	E 110 ° 21'04.1"
Burung	S 05 ° 53'20.1"	E 110 ° 20'29.1"

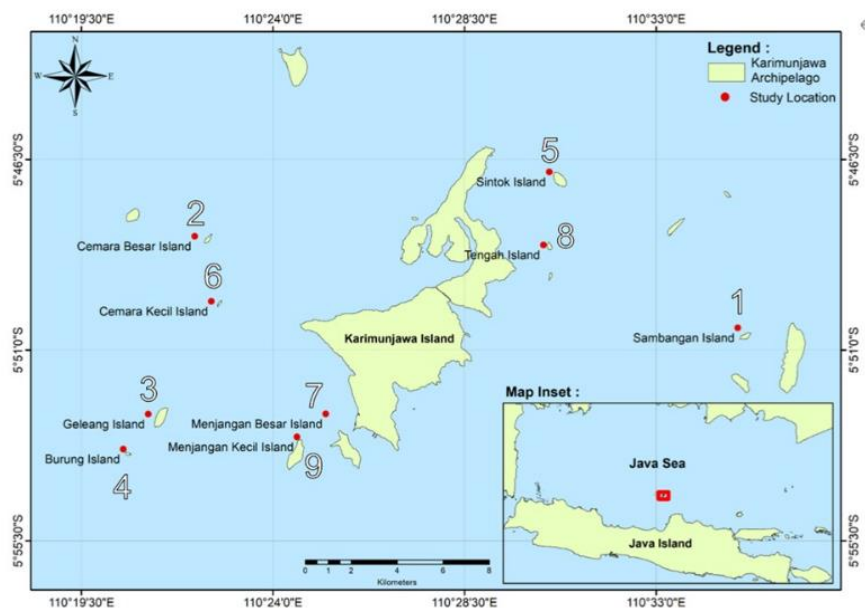


Figure 1. Map of the nine study islands in the Karimunjawa Archipelago, Central Java, Indonesia. Numbers indicate the rank of coral juvenile abundance among islands recorded in this study (see Figure 2).

During the survey, water quality parameters were measured at each site with 3 repetitions. Seawater temperature, salinity, pH, and dissolved oxygen were measured using a Hanna Instruments Multiparameter HI9829 (Hanna Instruments, Jakarta, Indonesia), and water visibility was assessed using a Secchi disk. The mean (\pm SD) values across all sites were as follows: 28.3 ± 0.47 °C (temperature), 9.28 ± 2.17 m (visibility), 34.15 ± 0.89 ppt (salinity), 8.12 ± 0.42 (pH), and 8.76 ± 1.44 mg.L⁻¹ (dissolved oxygen).

Hard coral (scleractinian) juveniles within each quadrat were identified from the photo quadrat images and classified into three size categories based on their maximum diameter: small (< 3 cm), medium (3 – 6 cm), and large (6–10 cm). Juvenile density was categorized into five classes: very low (0 – 2.5 colonies m⁻²), low (2.6–5 colonies m⁻²), moderate (5.1–7.5 colonies m⁻²), high (7.6–10 colonies m⁻²), and very high (> 10 colonies m⁻²) (Engelhardt, 2000). The dominant benthic groups within each quadrat were quantified as percentage cover using the software Coral Point Count with Excel extensions (CPCe) with 30 random points overlaid on each quadrat image (Kohler and Gill, 2006). Benthic categories and coral genera identification followed the Australian Institute of Marine Science (AIMS) ecosystem monitoring protocol (Jonker *et al.*, 2008) and included hard corals (Scleractinian) (HC), soft corals (SC), sponges (SP), macroalgae (MA), turf algae (TA), and crustose coralline algae (CCA).

Statistical analysis

Statistical analyses were conducted using R version 4.4.2. and RStudio version 2024.09.1+394 (R Core Team, 2024). The following packages were used: *performance* v0.13.0. (Hallam *et al.*, 2023), *glmmTMB* v1.1.10. (Nascimento *et al.*, 2025), *MuMIn* v1.48.4. (Martin *et al.*, 2025), and *emmeans* v1.10.7. (Lenth and Piakowski, 2025). Visualizations were produced using *ggplot2* v3.5.1. (Wickham *et al.*, 2016) and *ggeffects* v1.7.2. (Lüdtke, 2018).

To examine the factors influencing the abundance of hard coral juveniles (< 10 cm) per quadrat, zero-inflated generalized linear models (ZIGLMs) and zero-inflated generalized linear mixed models (ZIGLMMs) with a Poisson distribution to account for excess zero counts were applied. The models were built using *glmmTMB* (*glmmTMB*), with a single zero-inflation parameter applied to all observations ($\text{ziformula} = \sim 1$). In the ZIGLMMs, the island was included as a random effect. Model diagnostics were performed using the *performance* package, which included the following functions: *check_model()* to visually assess model assumptions, *check_collinearity()* to test for multicollinearity, *check_zero_inflation()* to evaluate zero-inflation, and

check_overdispersion() to assess overdispersion. Post-hoc pairwise comparisons were conducted using Tukey's test with the *emmeans()* function.

Variation in coral juvenile abundance among the nine islands was assessed using a ZIGLM with island as a fixed factor, followed by Tukey's post-hoc tests. The effects of benthic groups on juvenile abundance were examined using ZIGLMMs. Model selection was performed using the Akaike Information Criterion (AIC) using the *dredge()* function. The influence of hard coral cover on juvenile abundance was tested using a ZIGLMM, including hard coral cover as a fixed factor. Finally, the interaction between hard coral cover and island was examined using a ZIGLM, with hard coral cover, island, and their interaction as fixed factors.

Results and Discussion

The abundance of hard coral juveniles varied significantly among the nine islands of the Karimunjawa Archipelago (Figure 2, Table 2). This pattern closely corresponded with the ranking of total juvenile counts (Figure 1 and Figure 2). The three islands with the highest numbers and densities of juveniles were Sambangan Island (145 juveniles; 11.6 colonies.m⁻²), Cemara Besar Island (109 juveniles; 8.8 colonies.m⁻²), and Geleang Island (82 juveniles, 6.6 colonies.m⁻²). In contrast, the lowest number and density of juveniles were observed at Menjangan Besar Island (22 juveniles; 1.8 colonies.m⁻²), Menjangan Kecil Island (13 juveniles; 1.1 colonies.m⁻²), and Tengah Island (19 juveniles; 1.5 colonies.m⁻²). According to Engelhardt (2000), Sambangan Island was categorized as *very high*, Cemara Besar Island as *high*, Geleang Island as *moderate*, and Menjangan Besar Island, Tengah Island, and Menjangan Kecil Island as *low*.

This ranking revealed an interesting spatial pattern relative to the distance from the main Karimunjawa Island, with islands located farther from the main island exhibiting higher juvenile abundance of hard corals (Figure 1). Remote reefs may be less affected by pollution, sedimentation, and runoff associated with coastal development than coastal reefs. Anthropogenic stressors can significantly impact coral reproduction and recruitment processes, resulting in variations in coral juvenile abundance (Sawall *et al.*, 2013; Koester *et al.*, 2021). In the Karimunjawa Archipelago, human activities, including tourism, aquaculture, hotel operations, and port activities, are concentrated on Karimunjawa Island, making it the primary source of anthropogenic stress in the region (Aldyan *et al.*, 2023). In contrast, the outer islands generally have clearer waters and more favorable environmental conditions for coral recruitment than the inner islands. Supporting this

Table 2. Results of the zero-inflated generalized linear model (ZIGLM) with Tukey post-hoc tests showing significant differences ($p < 0.05$) in hard coral juvenile density (<10 cm) among the nine islands. Island abbreviations: Sam = Sambangan, CB = Cemara Besar, Gel = Geleang, Bur = Burung, Sin = Sintok, CK = Cemara Kecil, MB = Menjangan Besar, Ten = Tengah, MK = Menjangan Kecil.

Sam > Bur, Sin, CK, MB, Ten, MK
CB > Sin, CK, MB, Ten, MK
Gel > Sin, CK, MB, Ten, MK
Bur > MB, Ten, MK
Sin > MK

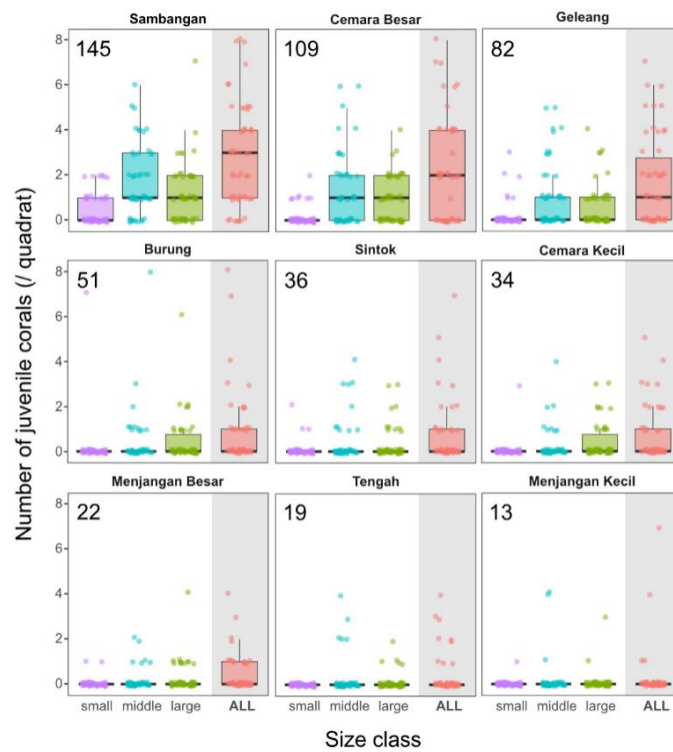


Figure 2. Hard coral juvenile densities at the nine islands in the Karimunjawa Archipelago in 2023. Size categories are small (0 – 3 cm), medium (3–6 cm), and large (6–10 cm). “ALL” represents all size classes combined. Total juvenile numbers per island are indicated in the upper left corner of each panel. Panels are arranged in descending order of juvenile abundance.

pattern, Drake *et al.* (2025) found higher coral juvenile densities in clear-water areas than in nutrient-rich, sediment-laden environments.

Most hard coral juveniles belonged to the medium (3–6 cm in diameter; 45%) and large size classes (6–10 cm; 43%), while only 12% were small (< 3 cm). The dominant genera were *Montipora* (49%), *Fungia* (20%), and *Porites* (6%). The predominance of medium- and large-sized juveniles of *Montipora* and *Fungia*, particularly in reefs located farther from the main island, likely reflects high survival rates through the early vulnerable stages under better habitat conditions. In contrast, the

scarcity of small juveniles suggests low recent recruitment (Bernard *et al.*, 2023; Isdianto *et al.*, 2024). This pattern may also be linked to substrate preferences (Figure 3) and the disturbance history of these reefs, as both *Montipora sp.* and *Fungia sp.* commonly colonize rubble derived from dead branching corals (Rasser and Riegl, 2002; Munasik *et al.*, 2016). Past events, such as coral bleaching, storms, or destructive fishing, may have generated rubble habitats that favor these genera.

Hard corals were the predominant benthic group across all islands, with median island-level cover ranging from 25% to 79% (Figure 4). The influence

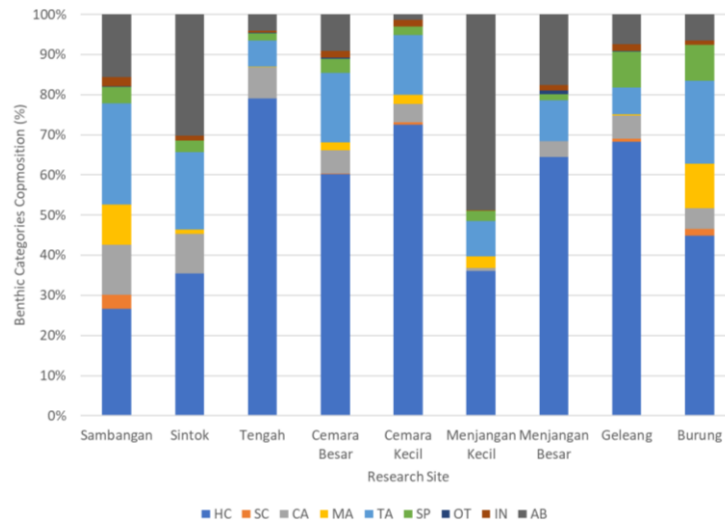


Figure 3. The distribution of benthic categories coverage composition among islands in Karimunjawa. HC = Hard Coral, SC = Soft Coral, CA = Coralline Algae, MA = Macro Algae, TA = Turf Algae, SP = Sponge, OT = Others, IN = Indeterminate, AB = Abiotic

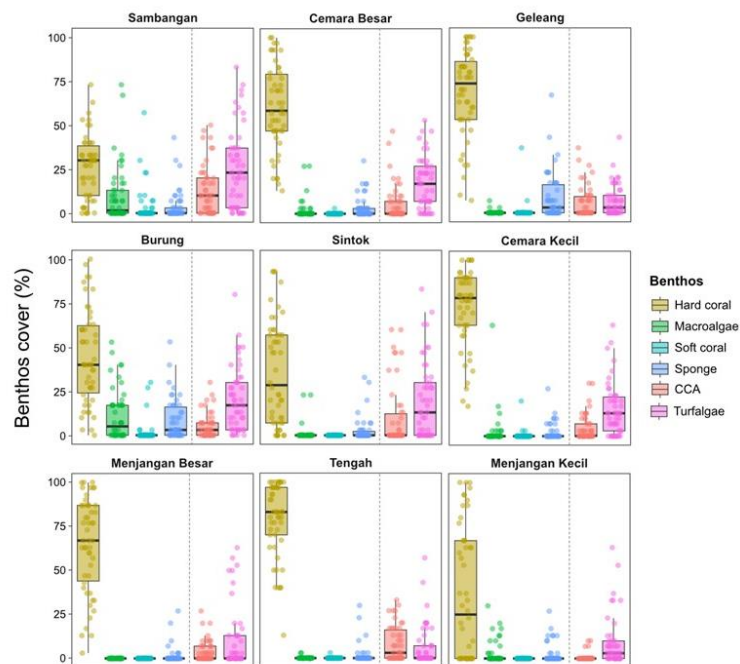


Figure 4. Benthos cover was recorded in the same quadrats used for juvenile counts across the nine study islands. Macro-benthos groups are separated from CCA and turf algae (TA) by a dotted line. Panels are arranged in descending order of juvenile abundance (see Figure 2).

of benthic composition on hard coral juvenile abundance (< 10 cm) was tested using ZIGLMMs. Among the six groups examined, only hard coral cover had a significant positive effect on juvenile abundance ($P = 0.03$; Figure 5). Model selection based on the AIC supported this finding, as hard coral cover was consistently retained in the five best-fitting models (Table 3). At the island scale, however, the positive relationship was significant only at Cemara

Besar and Sambangan ($P < 0.05$; Figure 6). This contrasts with previous studies that have reported a positive correlation between hard coral cover and juvenile density (Chiappone and Sullivan, 1996; Connell, 1973; Grigg and Maragos, 1974). One explanation is that high coral cover can reduce the available settlement space, whereas rubble-dominated reefs may provide settlement surfaces but limit post-settlement survival. Additional stressors,

such as sedimentation and poor water quality, may further constrain juvenile survival (Couch *et al.*, 2023; Isdianto *et al.*, 2024). The measured water-quality indicators at the sampling period were within commonly accepted ranges, which indicates there was no significant pollution during the period (Houk *et al.*, 2022) nor the effect of the monsoon on the nutrient input (Krisna *et al.*, 2025). However, coral larvae and newly settled juveniles may respond to

very local conditions, such as short sedimentation events after heavy rainfall, nearshore streams from coastal activities, or micro-scale turbidity (Tuttle and Donanue, 2022). This indicates that the measurements and the suite of parameters that were collected may not detect such a local condition. Therefore, periodic or small-scale sediment inputs, rather than sustained poor water quality, remain possible contributors to low juvenile survival at some sites.

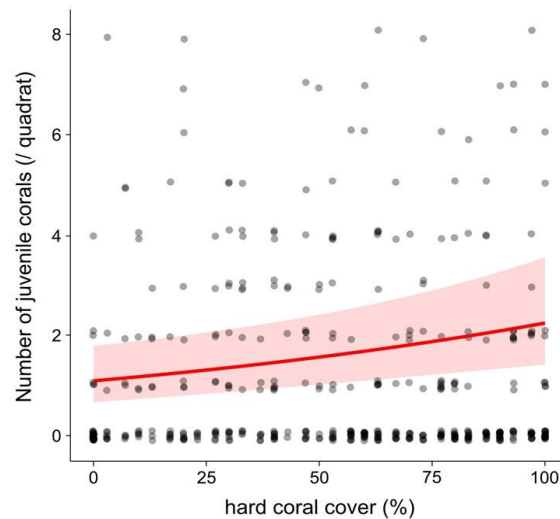


Figure 5. Relationship between hard coral cover and juvenile abundance (< 10 cm). The regression curve (line) with 95% confidence intervals (shaded area) was estimated using ZIGLMM. Points represent data across all size classes and islands.

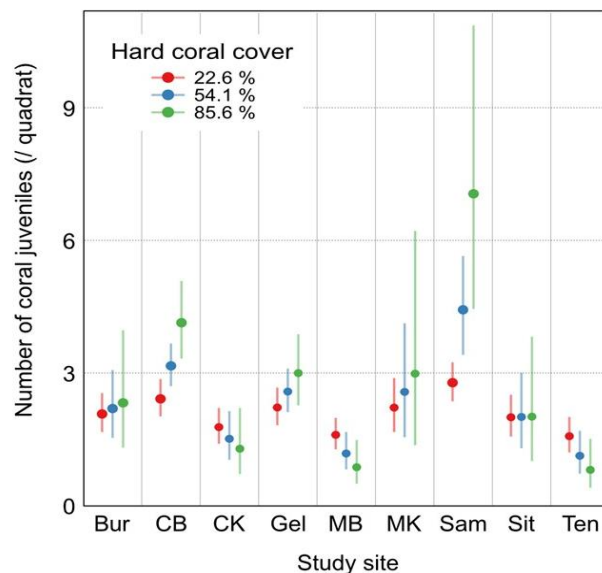


Figure 6. Effects of hard coral cover on juvenile abundance (< 10 cm) at each island. Estimated means with 95% confidence intervals (CIs) are shown for three levels of hard coral cover. A significant difference ($p < 0.05$) was detected only at Cemara Besar (CB) and Sambangan (Sam), where CIs do not overlap between low (22.6%) and high (85.6%) cover. Island abbreviations: Sam = Sambangan, CB = Cemara Besar, Gel = Geleang, Bur = Burung, Sin = Sintok, CK = Cemara Kecil, MB = Menjangan Besar, Ten = Tengah, MK = Menjangan Keci

Table 3. Model selection results for ZIGLMMs testing the effects of benthic groups on coral juvenile abundance. The five best models based on AIC are shown. Coefficients for selected benthic groups are presented in each model; empty cells indicate groups not selected.

Rank	Hard coral	Macro algae	Soft coral	Sponge	CCA	Turf algae	AIC	delta
1	0.0072						1234	0
2	0.0061					0.0044	1234.1	0.12
3	0.0076				0.0024		1235.7	1.76
4	0.0073	0.0010					1236	1.96
5	0.0073			0.0006			1236	1.99

Conclusion

This study revealed substantial spatial variation in hard coral juvenile abundance across nine islands in the Karimunjawa Archipelago, reflecting differences in reef recovery potential and exposure to human impacts. Juvenile densities were generally lower on islands closer to the main Karimunjawa Island, where human activities such as tourism, aquaculture, and port operations are concentrated, and higher on more remote islands. This suggests that anthropogenic stressors hinder coral recruitment. Juvenile assemblages were dominated by the genera *Montipora sp.* and *Fungia sp.*, primarily in medium-to large-size classes, likely reflecting local conditions, such as settlement substrates dominated by dead coral rubble and habitats that promote higher hard coral post-settlement survival. Although hard coral cover had an overall positive influence on juvenile abundance, the effect was significant only at Sambangan and Cemara Besar Islands, indicating that high coral cover alone does not ensure successful recruitment. These findings highlight the need for island-specific conservation and management strategies to enhance coral reef resilience throughout the Karimunjawa Archipelago.

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