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The effect of coral bleaching on the abundance, age
structure and juvenile settlement preferences of
Chaetodon octofasciatus



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Abstract

Coral reefs are responsible for facilitating the survival of many marine organisms through the provision of food, shelter and sites for juvenile fish recruitment, but are increasingly vulnerable to the impacts of global climate change. The mass coral bleaching event of 2023-2025 has affected tropical reef ecosystems worldwide. This study assessed trends in coral bleaching, corresponding population changes and juvenile settlement preferences of the obligate corallivore *Chaetodon octofasciatus* on the reefs of Koh Phangan, an island in the Gulf of Thailand, from 2023 to 2025. Benthic surveys and visual censuses were conducted across five reef sites on Koh Phangan in July and August 2025, and data collected was added to a long-term dataset from 2023 for statistical analysis. Bleaching prevalence remained constant, averaging 33% across the study period. *C. octofasciatus* population exhibited significant declines in biomass and adult abundance, but stable juvenile abundance. Juvenile settlement was rare, occurring exclusively on *Acropora* and *Pocillopora* and never on fully bleached colonies. Year and coral size exerted significant effects on the probability of juvenile presence within colonies and juvenile abundance respectively, but coral genus and bleach status did not. By providing information on the impacts of the 2023-2025 global bleaching event, this study emphasises the importance of using specialist species as bioindicators of environmental conditions and applying the knowledge gained to anticipate the effects of future disturbances on wider ecosystems.

Key words

Coral reefs · Climate change · Coral bleaching · Obligate corallivores · Chaetodontidae · *Chaetodon octofasciatus* · Juvenile recruitment

Abbreviations

Chaetodon octofasciatus (*C. octofasciatus*) · El Niño Southern Oscillation (ENSO) · National Oceanic and Atmospheric Administration (NOAA) · Centre for Oceanic Research and Education | Southeast Asia (COREsea) · Standard error (SE)

1. Background

Coral reefs are the most unique and productive ecosystems on our planet (Reaka-Kudla, 1997). Despite covering less than 1% of the ocean floor, coral reefs support 25% of all marine organisms (Pratchett *et al.*, 2004). They are highly complex heterogenous habitats that offer an abundance of shelter and food resources (Cole and Pratchett, 2011), and are thus aptly titled “rainforests of the sea” (Reaka-Kudla, 1997). The high coral species diversity and spatial cover within reefs generates a topographical complexity that can sustain exceptionally rich and diverse ecological communities (Coker *et al.*, 2009). Live Scleractinian (hard) corals form the foundation of tropical reef ecosystems (Cole and Pratchett, 2011) and are critical components of benthic habitats (Coker *et al.*, 2009). Variations in coral composition and growth form shape the substrate topography of reefs, creating mosaics of microhabitats that promote niche specialisation exploited by many organisms, particularly fish (Coker *et al.*, 2009; Fakan *et al.*, 2024). As sources of refuge and foraging opportunities, structurally complex coral systems mediate key ecological processes, such as competition and predation, which underscores their importance to reef fish communities (Coker *et al.*, 2009). Therefore, disturbance events that act to reduce coral cover and diversity are expected to have profound effects on marine organisms and the stability of the ecosystem.

Coral reefs are among the world’s most vulnerable ecosystems (Pratchett *et al.*, 2015), with climate change representing their most significant and rapidly intensifying threat (Coker *et al.*, 2009). The

health and long-term viability of coral reefs have already been compromised by extensive degradation driven by coral bleaching, disease, changing sea levels, and ocean acidification (Wilson *et al.*, 2013; Van Nguyen *et al.*, 2024; Coker *et al.*, 2009). The frequency, spatial extent and severity of these disturbances continue to increase globally (Wilson *et al.*, 2013), most strikingly so for coral bleaching (Cole *et al.*, 2014). Bleaching is triggered in response to thermal stress, when ambient water temperatures exceed bleaching threshold temperature of corals, typically 1 °C above baseline levels (NOAA Coral Reef Watch, 2025a). This causes corals to expel their endosymbiotic dinoflagellates (zooxanthellae), resulting in the visible paling or whitening of coral polyps (Cole *et al.*, 2014; Lesser, 2011). Corals are sensitive to accumulating heat stress, therefore, if elevated temperatures persist over prolonged periods, coral mortality may ensue (NOAA Coral Reef Watch, 2025a; McCormick *et al.*, 2010). Following coral death, turf algae rapidly colonises the coral skeleton, increasing its susceptibility to erosion and structural collapse (Coker *et al.*, 2009). When occurring on a large scale, this results in marked reductions of the spatial extent and structural complexity of reef habitats (Boström-Einarsson *et al.*, 2014; Cole *et al.*, 2014).

Global climatic conditions, such as the El Niño Southern Oscillation (ENSO), play a central role in determining the frequency and severity of bleaching events (Lesser, 2011). This is a naturally occurring climate phenomenon dominating global climate variation, specifically sea surface temperatures (Jiang *et al.*, 2025). It is characterised by two distinct phases: the warm El Niño phase and cool La Niña phase. These cyclically occur every 2 to 7 years and vary in severity (Jiang *et al.*, 2025); however, the frequency of future extreme El Niño events is predicted to double with increasing anthropogenic disturbance (Claar *et al.*, 2018; Jiang *et al.*, 2025). El Niño events manifest as episodic pulses of intense heat stress; these short-term periods of rapid warming can exceed the thermal tolerance of corals and trigger bleaching (Claar *et al.*, 2018). All mass bleaching events recorded in recent decades have coincided with extreme El Niño events, notably those of

1997-1998, 2015-2016 and 2023-2025, during which estimated coral mortality exceeded 90% in parts of the Eastern Pacific and Indian Oceans (Claar *et al.*, 2018; Jiang *et al.*, 2025). In 2024, the National Oceanic and Atmospheric Administration (NOAA) confirmed the world was experiencing the fourth and largest global coral bleaching event to date, impacting 84% of global coral reef area (NOAA Coral Reef Watch, 2025b).

The fragmentation, degradation and loss of coral reef habitats are expected to have disproportionate impacts on specific coral species (Coker *et al.*, 2009). Many reef fish depend on Scleractinian coral species that are highly susceptible to bleaching, such as *Acropora* and *Pocillopora* (Coker *et al.*, 2009). The loss of these structurally complex corals reduces critical resource quality and availability and exacerbates competition, compromising the survival, growth and reproductive success of reef fish (Boström-Einarsson *et al.*, 2014). This habitat degradation exerts the most severe impacts on highly specialised, coral-dependent fish species, threatening local population extinctions (McCormick *et al.*, 2010) and ecosystem diversity (Cole *et al.*, 2014).

The condition of coral determines its suitability as a habitat for marine organisms. This influences the settlement success and long-term persistence of populations, as many coral reef fish select specific coral microhabitats as juveniles and remain associated with them throughout adulthood (Bonin *et al.*, 2009). Fish rely on sensory cues (chemical, auditory, visual and thermal) to assess coral health, condition and overall suitability (Coppock *et al.*, 2013). This allows them to settle on corals that confer the best chance of survival, and avoid bleached, dead or degrading corals.

Nonetheless, even on healthy reefs, suitable corals are a limiting resource (Boström-Einarsson *et al.*, 2014). As a result, declines in the abundance or condition of corals will have detrimental cascading effects on fish populations (Coker *et al.*, 2009; McCormick *et al.*, 2010). Reduced coral cover has been associated with drops in fish species density and richness (Coppock *et al.*, 2013), particularly among highly specialised, coral-dependent species. Unlike generalist species,

specialists occupy narrow ecological niches and exhibit limited behavioural and dietary flexibility, making them particularly vulnerable to fluctuations in resource availability and environmental conditions (Pratchett, 2013; Pratchett *et al.*, 2013). Consequently, these species face elevated risk of population collapse or extinction during times of disturbance (Pratchett *et al.*, 2013; Cole *et al.*, 2014). Specialist life-history strategies are common in organisms inhabiting complex environments, due to the abundance and diversity of niches available (Bonin *et al.*, 2009). Butterflyfish (family *Chaetodontidae*) are a prime example of highly specialised fishes (Pratchett *et al.*, 2013; Cole and Pratchett, 2013; Van Nguyen *et al.*, 2024). Eight-banded butterflyfish (*Chaetodon octofasciatus*) are one of the most specialised within this family. They are classified as *obligate corallivores*, referring to their near-exclusive dependence on branching coral species, notably *Acropora* and *Pocillopora*, for food and settlement, preferentially selecting these over more structurally simple or abundant coral species (Pratchett, 2013; Pratchett *et al.*, 2013).

One of the most important life history transitions for coral reef fish occurs when juveniles complete their pelagic larval stage and settle onto the reef, integrating into the benthic population (McCormick *et al.*, 2010; Van Nguyen *et al.*, 2024). This process is known as *recruitment* and is a vital element in maintaining population size and distribution. Continuous and reliable juvenile input into a population is necessary to compensate for adult mortality and prevent population decline during times of disturbance (Caley *et al.*, 1996). The abundance and distribution of recruits are influenced by predation, habitat structure and resource availability (Wilson *et al.*, 2013; Van Nguyen *et al.*, 2024), with vulnerability to environmental stressors and predation primary sources of juvenile mortality (Fakan *et al.*, 2024). Branching corals, typically *Acropora* and *Pocillopora*, are key settlement habitats for juvenile *C. octofasciatus* (Pratchett, 2013). Their physically complex branching structure, in addition to the chemical defences and stinging nematocysts of coral tissue, act as physical deterrents to predators, thereby promoting odds of juvenile survival (Coker *et al.*,

2009; Cole and Pratchett, 2011; Pratchett *et al.*, 2013). *C. octofasciatus* juveniles are territorial and highly site-attached and, following initial settlement, will rarely move from their chosen colony (Cole and Pratchett, 2011). Therefore, the selection of a suitable habitat is a critical determinant of juvenile survival (McCormick *et al.*, 2010). Settlement onto structurally or nutritionally sub-optimal habitats may increase exposure to predators (McCormick *et al.*, 2010) as well as negatively impact growth, body condition and future success, ultimately reducing recruitment viability and adult *C. octofasciatus* populations (Coppock *et al.*, 2013).

Considering the widespread importance of coral reef ecosystems, continual monitoring is imperative for assessing changes in their condition, biodiversity, productivity and overall integrity (Samoilys *et al.*, 2025). Indicator species offer one such means (Madduppa *et al.*, 2014), as their interactions with the environment and responses to change can help provide a comprehensive overview of ecosystem function and sensitivity to disturbances (McCormick *et al.*, 2010). To reliably inform coral condition, indicator species must exhibit clear and observable responses to declines in coral quality and cover (Samoilys *et al.*, 2025). Abundance and size-based metrics present a simple and cost-effective means of attaining such information (Samoilys *et al.*, 2025; Crosby *et al.*, 2013). Owing to their obligate coral dependence, *C. octofasciatus* have been proposed as an indicator species of coral reef condition (Taira *et al.*, 2016; Samoilys *et al.*, 2025). Inhabitants of coral reefs from 3 to 20 metres depth across the Indo-West Pacific, *C. octofasciatus* are characterised by deep, compressed bodies, protruding mouths and eight distinctive black stripes across a white and yellow body; adults grow to a maximum length of approximately 12 cm with juveniles smaller than 3.5 cm (FishBase, 2024). The abundance, specificity and distinctive appearance of *C. octofasciatus* justifies their consideration as an ideal indicator and study species. Climate-driven coral bleaching is expected to elicit strong effects on coral reef fish species by degrading habitat quality and food availability. This study explores the ecological consequences of

coral bleaching on the obligate corallivorous butterflyfish *Chaetodon octofasciatus* on reefs surrounding Koh Phangan, Gulf of Thailand, between 2023 and 2025. It aims to investigate changes in coral bleaching extent, *C. octofasciatus* population structure, abundance and biomass, and juvenile settlement patterns.

Despite shifts towards cooler climate patterns following the 2023-2025 El Niño event, ongoing global warming is anticipated to have driven continued increases in bleaching across reefs, accompanied by declines in the biomass and abundance of both adult and juvenile *C. octofasciatus*. Additionally, juveniles are expected to settle non-randomly within large, unbleached branching coral colonies as indicators of the colony's good condition. These predictions reflect the dependence of *C. octofasciatus* on live coral and highlight the vulnerability of this species to continued bleaching-driven habitat degradation.

2. Methods

2.1 Study site

The study was conducted from the 15th July to 26th August 2025 on the island of Koh Phangan, located in the lower Gulf of Thailand, approximately 60 km north-east of mainland Thailand. Data collection was carried out across five reef sites on the north and northwest coast of Koh Phangan. These sites included Haad Salad (HS), Mae Haad 4 (MH4), Ao Thong Lang (ATL), Chaloklum Bay East (CBE) and Haad Khom (HK) (Fig. 1). This study was conducted in collaboration with the Centre for Oceanic Research and Education | Southeast Asia (COREsea), which has been conducting long-term monitoring and research on the coral reef systems of Koh Phangan since 2011.

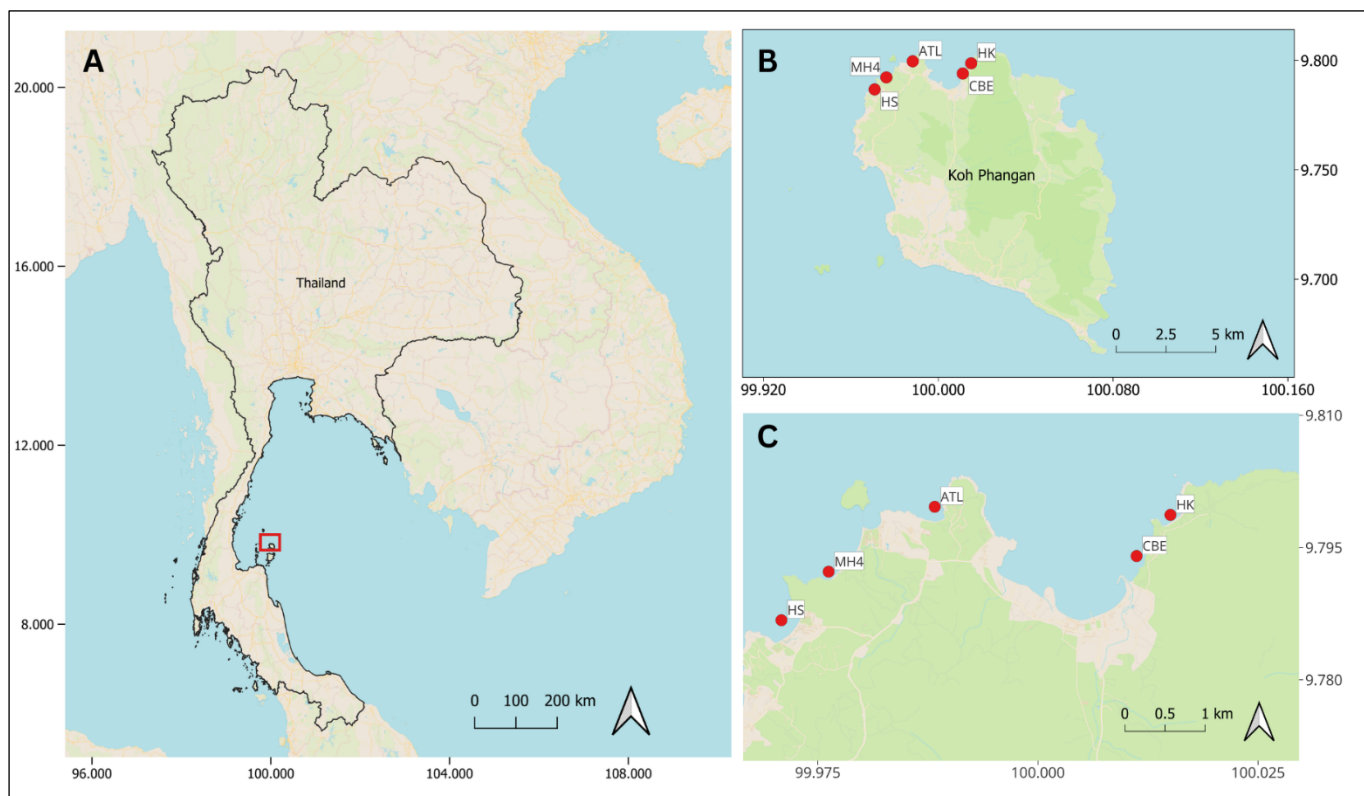


Figure 1. A) Map of Thailand, red box indicating location of Koh Phangan; **B)** map of Koh Phangan located in the Samui archipelago in the Gulf of Thailand; **C)** the five surveyed reef sites: HS = Haad Salad (9.786°N, 99.970°E), MH4 = Mae Haad 4 (9.792°N, 99.976°E), ATL = Ao Thong Lang (9.778°N, 99.675°E), CBE = Chaloklum Bay East (9.794°N, 100.011°E), HK = Haad Khom (9.799°N, 100.015°E). Map produced in QGIS version 3.44.7-Solothurn (QGIS Development Team, 2025). Background tiles provided by CARTO (2025), based on data from OpenStreetMap contributors (2025). National boundary shapefile taken from UNOCHA (2019), sourced from the Royal Thai Survey Department.

2.2 Data collection

SCUBA-based surveys were conducted following methodology employed by COREsea, comprising three 50 m x 5 m (250 m²) belt transects spaced 1-2 metres apart (Fig. 2) randomly positioned parallel to the coastline following the reef crest (4-6 m depth). Surveys were carried out between 11:00 and 13:00 each day, to ensure consistency in fish activity and behaviour and reduce temporal variability across study sites. These protocols were consistent with those used during

2023 and 2024 data collection. All data collected was added to COREsea's long-term monitoring dataset, allowing trends from previous years to be identified.

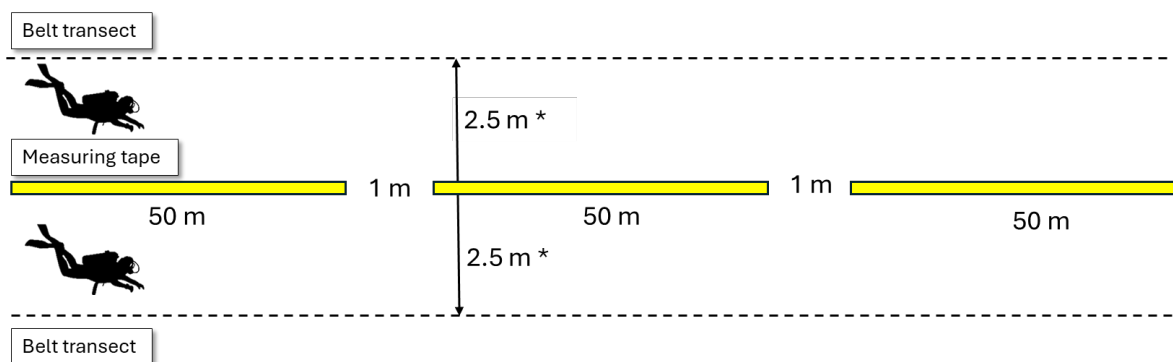


Figure 2. Diagram of belt transect methodology. Yellow lines represent the 50 metre transect measuring tapes. Dotted lines represent the transect belt (edge of transect). * 2.5 metres either side of the transect creates a total belt width of 5 metres, 1 metre either side of the transect creates a 2 metre belt.

2.3 Abundance and sizing survey

Underwater visual census techniques were employed to assess *C. octofasciatus* abundance and size. Within each transect, SCUBA divers recorded all *C. octofasciatus* encountered within the 5 m belt. The same divers conducted every survey to minimise error. To estimate individual lengths, divers approached fish as closely as possible and used a scale on a dive slate to record total length to the nearest centimetre. Total length was measured from tip of mouth to longest end of caudal fin. Individuals less than 3 cm were classed as juveniles, while those over 3 cm were classed as adults (Fig. 3). Individual mass was estimated using the length – weight relationship (Kulbicki *et al.*, 2005):

$$W = a L^b$$

Where *W* is the individual mass in grams (g), *L* is the total length in centimetres (cm), and *a* and *b* are parameters estimated by regression from measured specimens. As no length-weight parameters were available specifically for *C. octofasciatus*, values derived for genus *Chaetodon*

spp. were taken from Kulbicki *et al.* (2005), where $a = 0.0450$ and $b = 2.814$. Individual mass estimates were summed per transect to calculate total population biomass per 250 m².

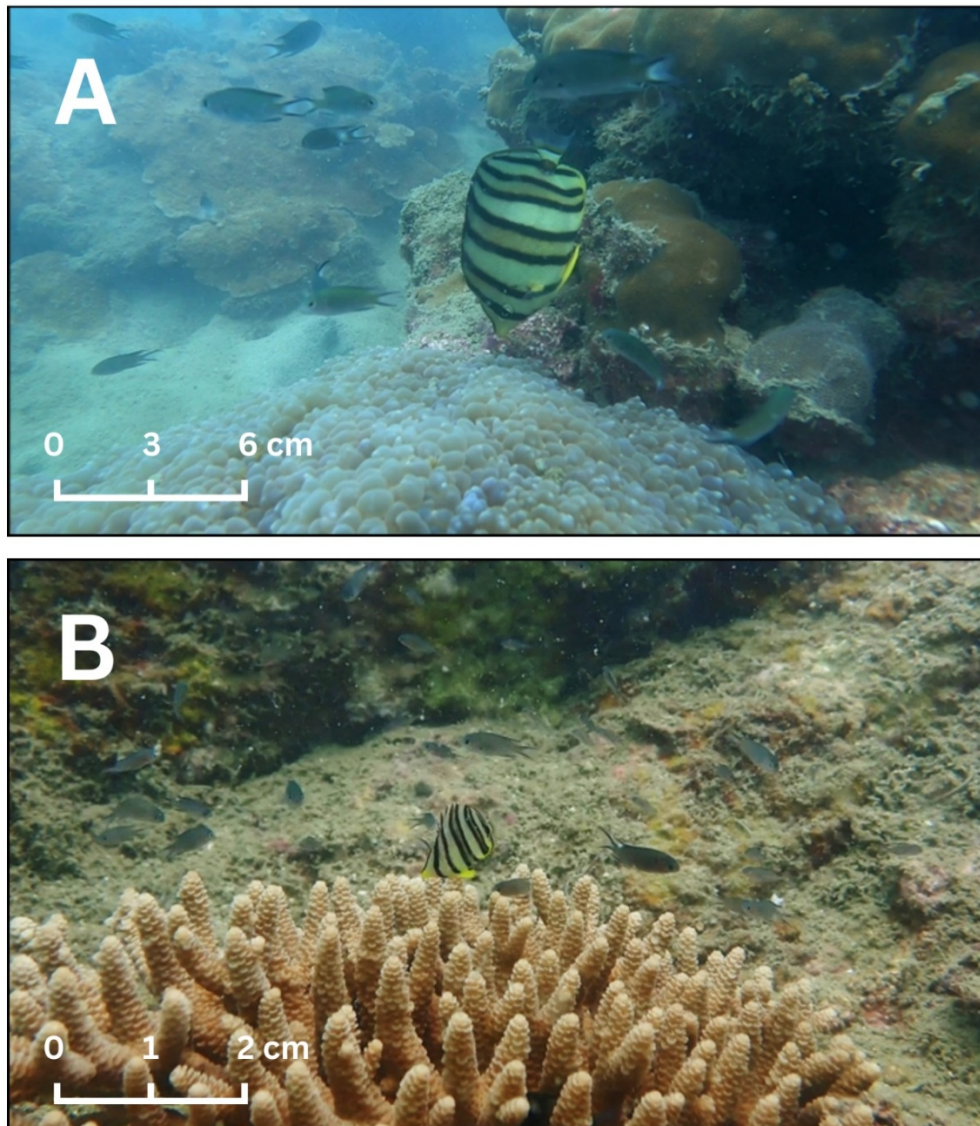


Figure 3. *Chaetodon octofasciatus* in Mae Haad 4 reef site, Koh Phangan, Gulf of Thailand. **A** shows a feeding adult; **B** shows a resident juvenile within an *Acropora* colony. Photographs by author (2025).

2.4 Resident juvenile survey

Concurrent with the visual census of *C. octofasciatus*, an assessment of the resident juvenile population was conducted. All branching coral colonies within each transect were visually examined. For each branching colony found, coral genus, bleaching status, maximum diameter to the nearest centimetre and number of resident juveniles, if any, were recorded. Bleaching status

was classified as non-bleached, partially bleached or fully bleached. Non-bleached colonies showed normal tissue colouration; fully bleached colonies exhibited complete whitening of the tissue; partially bleached colonies were any intermediate state between these extremes (Fig. 4).

2.5 Bleaching survey

Coral bleaching surveys were conducted alongside the fish and resident juvenile surveys along the same transects but using belt transects measuring 50 m x 2 m (100 m²). Within this belt, all coral colonies were counted and categorised by growth form (massive, branching, plating, solitary) and bleaching status (non-bleached, partially bleached, fully bleached) (Fig. 4). Counts of partially and fully bleached colonies were summed to produce the total number of bleached colonies. The prevalence of bleaching was calculated as the proportion of bleached colonies relative to the total number of colonies surveyed.



Figure 4. *Acropora* colonies of different bleaching states. **A)** non-bleached colony (Koh Phangan, Gulf of Thailand, photograph by author (2025)); **B)** partially bleached colony (COREsea, 2025); **C)** fully bleached colony (Koh Tao, Gulf of Thailand, photograph by author (2024)).

2.6 Statistical analyses

All statistical analyses and graphical representations were carried out in R version 4.5.2 (R Core Team, 2025). A series of Generalised Linear Mixed Effects Models (GLMMs) were fitted using the *glmmTMB* R package (Brooks *et al.*, 2017). Model distributions were selected according to the

nature of each response variable and model fit using R package *DHARMa* (Hartig, 2024). The best fitting model, following testing contributions of fixed and random effects, was selected by comparing AIC values, distributional fit (Kolmogorov-Smirnov test), dispersion and outliers using the *performance* R package (Lüdecke *et al.*, 2021.) The most parsimonious model was retained (see Appendix Table 1). Reef site and survey date were specified as random effects to account for baseline differences among reef sites and repeated sampling. Where random effects caused convergence failures or did not meaningfully improve model fit, they were excluded from the final model. Type II Wald chi-square tests were used to assess the significance of fixed effects in models without interaction terms, and Type III Wald chi-square tests were used in models containing interaction terms. Post-hoc pairwise comparisons were conducted using the *emmeans* package (Lenth and Piaskowski, 2025) to identify significant differences between factor levels. For all analyses, p-values of less than 0.05 were considered statistically significant.

Bleaching prevalence across years was modelled using a GLMM with a beta distribution and a logit link function. To ensure temporal consistency and capture trends in peak bleaching on Koh Phangan across years (V.Fahey, pers.comm., 2026), analysis was restricted to data collected between April and August. Differences in *C. octofasciatus* biomass across years were modelled using a GLMM with a Gaussian distribution. *C. octofasciatus* abundance was modelled using a negative binomial distribution, with life stage (adult vs. juvenile) and year included as fixed effects along with their interaction term. The number of juvenile *C. octofasciatus* per coral colony was modelled using a Poisson distribution, with colony size and bleaching status included as fixed effects along with their interaction term. Despite not producing the most parsimonious model, bleaching status was retained as a fixed effect to explicitly test its influence on juvenile settlement when controlling for colony size. A prediction plot was used to visualise the results using the *ggeffects* R package (Lüdecke, 2018). To examine the probability of juvenile settlement, juvenile

counts were converted to a binary presence or absence variable prior to modelling. The probability of juvenile presence within coral colonies was modelled using a binomial distribution, with coral genus, bleaching status, and year included as fixed effects. The *ggplot2* R package (Wickham, 2016) was used to visualise all plots.

3. Results

A total of 610 transects were surveyed from 2023 to 2025 across the five reef sites, comprising 377 bleaching surveys, 186 *C. octofasciatus* sizing surveys and 47 juvenile settlement surveys. During this period, 5,785 *C. octofasciatus* (5,185 adults and 600 juveniles) were recorded and sized, with a minimum recorded size of 0.5 cm and maximum of 14.0 cm. Mean juvenile size was 2.19 ± 0.03 cm SE and mean adult size was 6.85 ± 0.02 cm SE. A total of 1,583 branching coral colonies were surveyed (1,386 *Acropora*, 197 *Pocillopora*), of which 40 colonies (2.53%) hosted at least one juvenile (38 *Acropora*, 2 *Pocillopora*). Among occupied colonies, mean juvenile abundance was 2.6 (range 1 - 9). Mean coral colony size was 27.03 cm (range 2 - 190 cm). No juveniles were observed on any fully bleached corals or *Porites* corals; these colonies were therefore excluded from analysis.

3.1 Bleaching prevalence

Over the three years, the proportion of corals bleached on the reefs ranged from 1% to 86%. Bleaching prevalence did not differ significantly across the peak bleaching months (April to August) between 2023 and 2025 ($\chi^2 = 0.319$, $df = 2$, $p > 0.05$) (Fig. 5). The mean proportion of colonies bleached was relatively similar across years: $32.51\% \pm 3.01\%$ SE in 2023, $33.32\% \pm 1.86\%$ SE in 2024 and $33.73\% \pm 2.15\%$ SE in 2025 (see Appendix Table 2a).

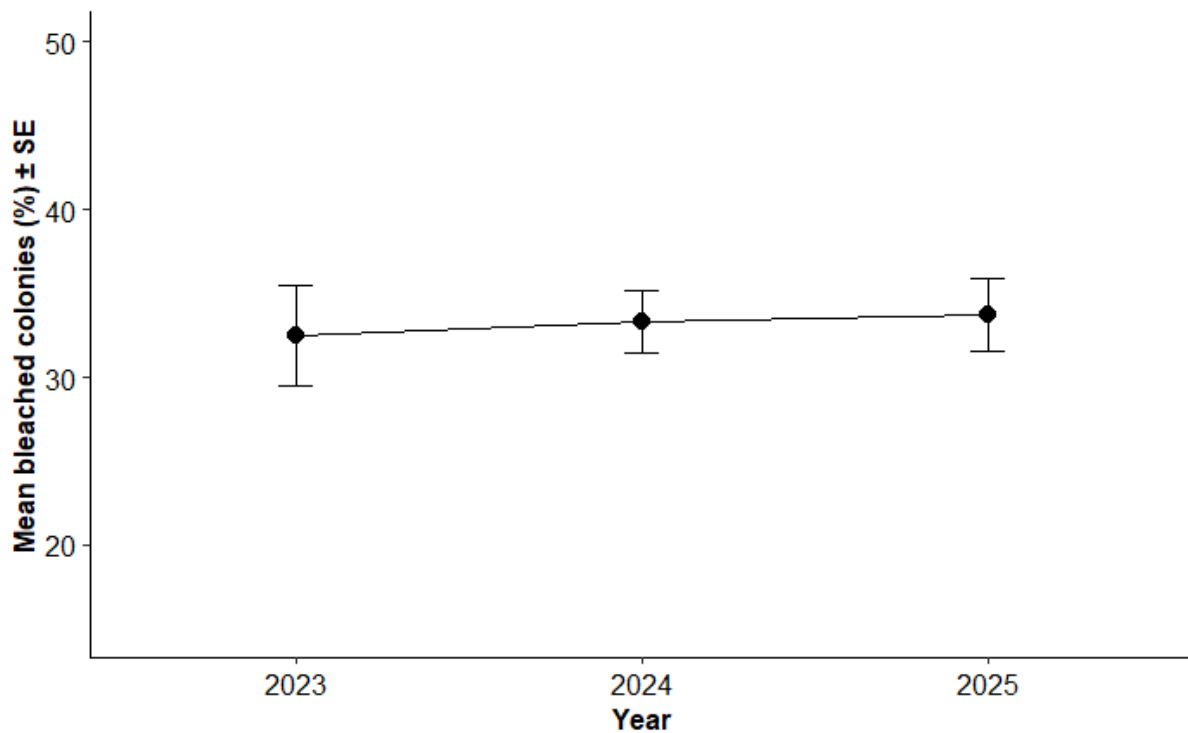


Figure 5. Mean percentage ($\pm$ standard error) of bleached coral colonies (per 100m² area) from 2023 to 2025 across all surveyed reef sites on Koh Phangan, Gulf of Thailand.

3.2 *Chaetodon octofasciatus* biomass and abundance

Mean *C. octofasciatus* population biomass differed between years ($\chi^2 = 103.53$, $df = 2$, $p < 0.001$) (Fig. 6). Biomass was highest in 2023 (395.39 ± 15.05 SE g per 250m²), declined significantly in 2024 (342.10 ± 16.72 g per 250m² SE; $z = 2.552$, $p < 0.05$), and decreased further in 2025 (210.35 ± 11.39 SE g per 250m²; $z = 9.746$, $p < 0.001$) (see Appendix Table 2b). Overall, mean biomass declined by 47% across the three-year period.

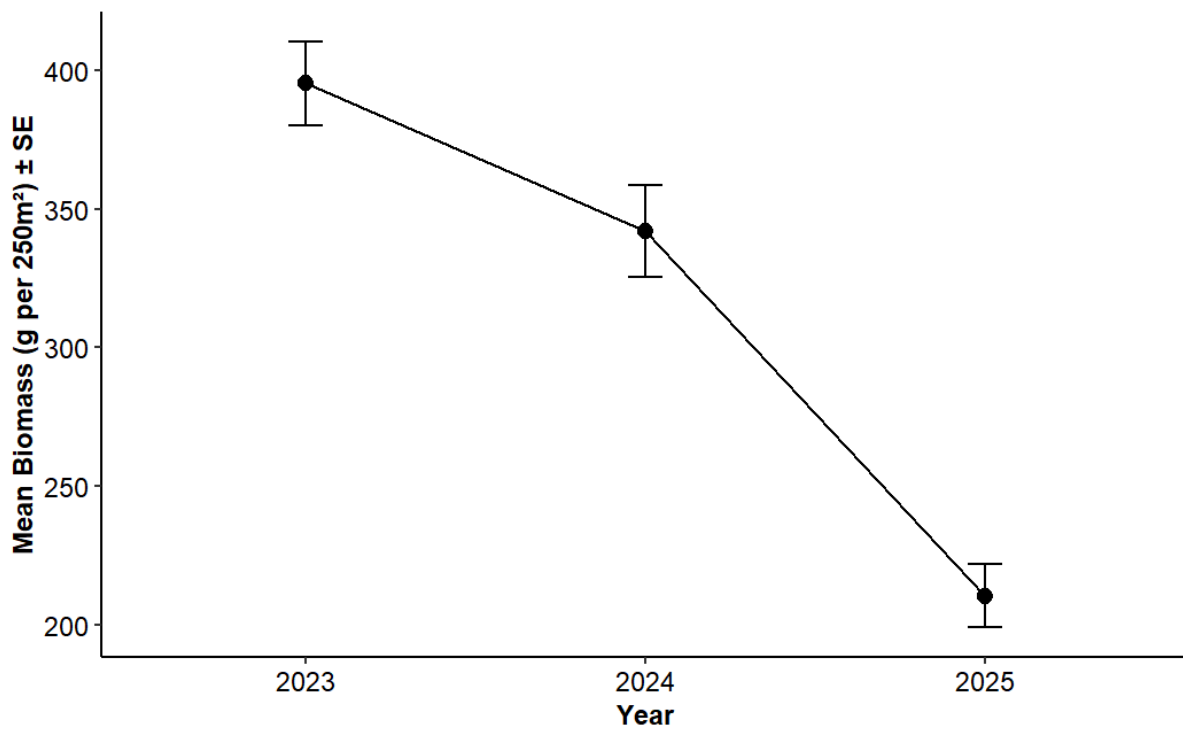


Figure 6. Mean biomass (grams $\pm$ standard error) of *Chaetodon octofasciatus* populations (per 250m² area) from 2023 to 2025 across all surveyed reef sites on Koh Phangan, Gulf of Thailand.

Adult *C. octofasciatus* abundance differed significantly between years ($\chi^2 = 56.59$, $df = 2$, $p < 0.001$) (Fig. 7). Mean adult abundance remained similar between 2023 (33.53 ± 1.22 SE individuals per 250 m²) and 2024 (30.29 ± 1.16 SE individuals per 250 m²) ($z = 1.527$, $p > 0.05$), before declining sharply to 21.71 ± 1.00 SE individuals per 250 m² in 2025. This reduction was significant relative to both 2023 ($z = 7.210$, $p < 0.001$) and 2024 ($z = 5.334$, $p < 0.001$) (see Appendix Table 2c). Overall, mean adult abundance dropped by 35.3% across the study period.

In contrast, mean juvenile abundance did not significantly differ between years ($\chi^2 = 3.25$, $df = 2$, $p > 0.05$) (Fig. 7). While abundance appeared to decrease from 2023 to 2024, then increase in 2025, no differences between years were significant (see Appendix Table 2c).

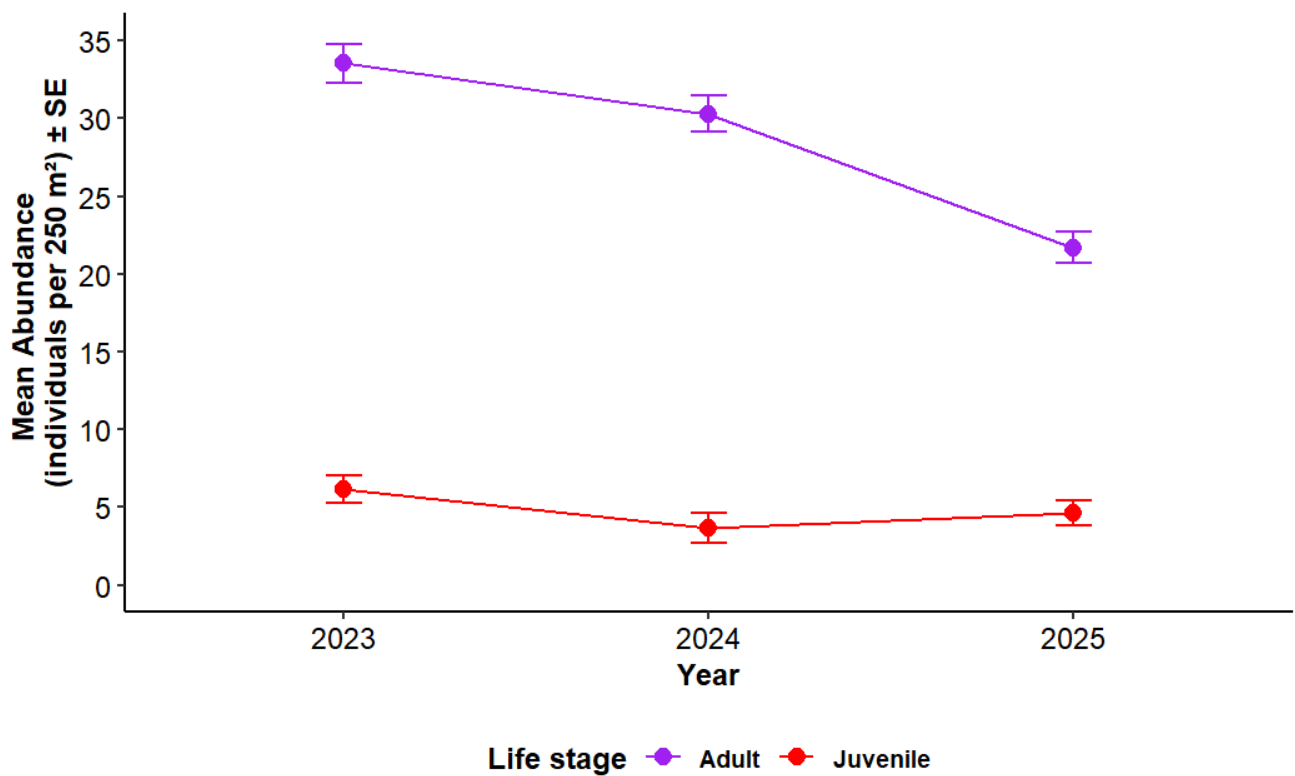


Figure 7. Mean abundance ($\pm$ standard error) of *Chaetodon octofasciatus* adults (purple line) and juveniles (red line) (per 250m² area) from 2023 to 2025 across all surveyed reef sites on Koh Phangan, Gulf of Thailand.

3.3 Settlement preferences of juvenile *Chaetodon octofasciatus*

Colony size was a significant predictor of the number of resident juveniles ($\chi^2 = 14.376$, $df = 1$, $p < 0.001$), with larger coral colonies consistently supporting more juveniles (Fig. 8). This relationship held for both non-bleached ($z = 3.792$, $p < 0.001$) and partially bleached colonies ($z = 3.039$, $p < 0.01$). Non-bleached colonies appeared to support a higher abundance of juveniles per colony than partially bleached colonies, but this difference was non-significant ($\chi^2 = 0.218$, $df = 1$, $p > 0.05$). The interaction between colony size and coral bleaching status was also non-significant ($\chi^2 = 0.473$, $df = 1$, $p > 0.05$), indicating that bleaching does not alter how juvenile abundance scales with colony size (Table 1).

Table 1. Results of GLMM (Poisson) examining the effects of colony size and bleaching status on juvenile *C. octofasciatus* number per coral colony.

Variable	χ^2	df	p
Colony size	14.376	1	<0.001
Bleaching status	0.218	1	0.640
Colony size × Bleaching status	0.473	1	0.492

Note: Type III Wald chi-square tests. Residual df = 34. **Bold** p-values indicate statistical significance ($p < 0.05$).

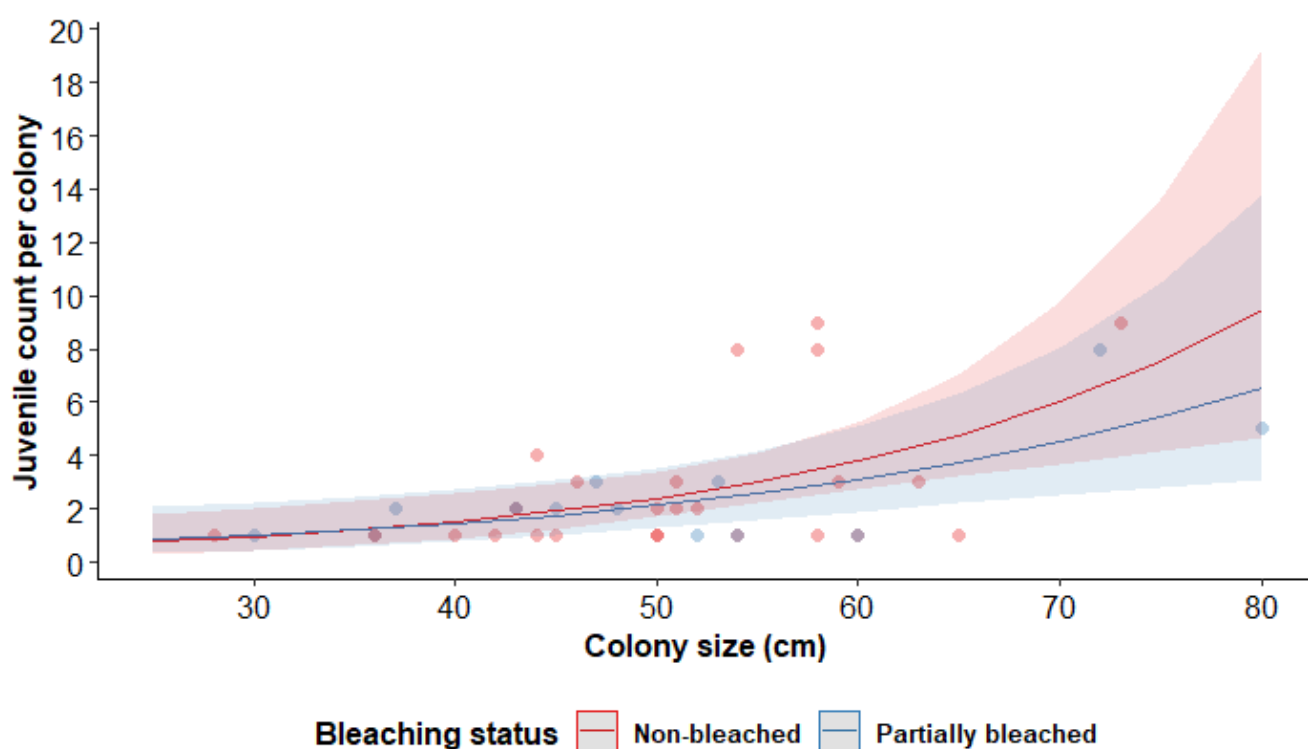


Figure 8. Prediction plot visualising the relationship between number of resident juveniles and colony size for non-bleached and partially bleached branching corals (*Acropora*, *Pocillopora*). Red represents non-bleached coral; blue represents partially bleached coral. Points indicate data points collected in the field. Solid lines indicate model regression lines. Shaded areas indicate confidence intervals.

Colonies hosting resident juveniles were rare overall, with *Acropora* accounting for the majority of colonies surveyed and colonies hosting juveniles, compared to *Pocillopora* (see Appendix Table 2). No juveniles were recorded on fully bleached colonies for either genus, or on any *Porites* colonies surveyed.

The probability of juvenile presence differed significantly between years ($z = 2.848$, $p < 0.005$), with colonies in 2025 showing 3.3 times higher probability of juvenile presence than 2024 (odds ratio = 3.30, 95% CI: 1.45 – 7.51). Predicted probability of juvenile presence was 0.82% (95% CI: 0.27 – 2.47%) in 2024, increasing significantly to 2.64% (95% CI: 1.06 – 6.46%) in 2025. This temporal pattern was most pronounced in non-bleached *Acropora* colonies, which showed the greatest rise in observed juvenile presence between 2024 and 2025 (Fig. 9).

Pocillopora colonies showed 76% lower odds of juvenile presence than *Acropora* colonies, however, this was non-significant (odds ratio = 0.235, $z = -1.929$, $p > 0.05$). Predicted probability of juvenile presence was 3.0% per colony (95% CI: 1.49–5.91%) in *Acropora* and 0.72% (95% CI: 0.16–3.27%) in *Pocillopora* (Fig. 9).

Bleaching status had no significant effect on the probability of juvenile presence ($z = -1.342$, $p > 0.05$). Non-bleached colonies had a predicted juvenile presence probability of 1.86% (95% CI: 0.70–4.86%) compared to 1.17% (95% CI: 0.42–3.18%) for partially bleached colonies.

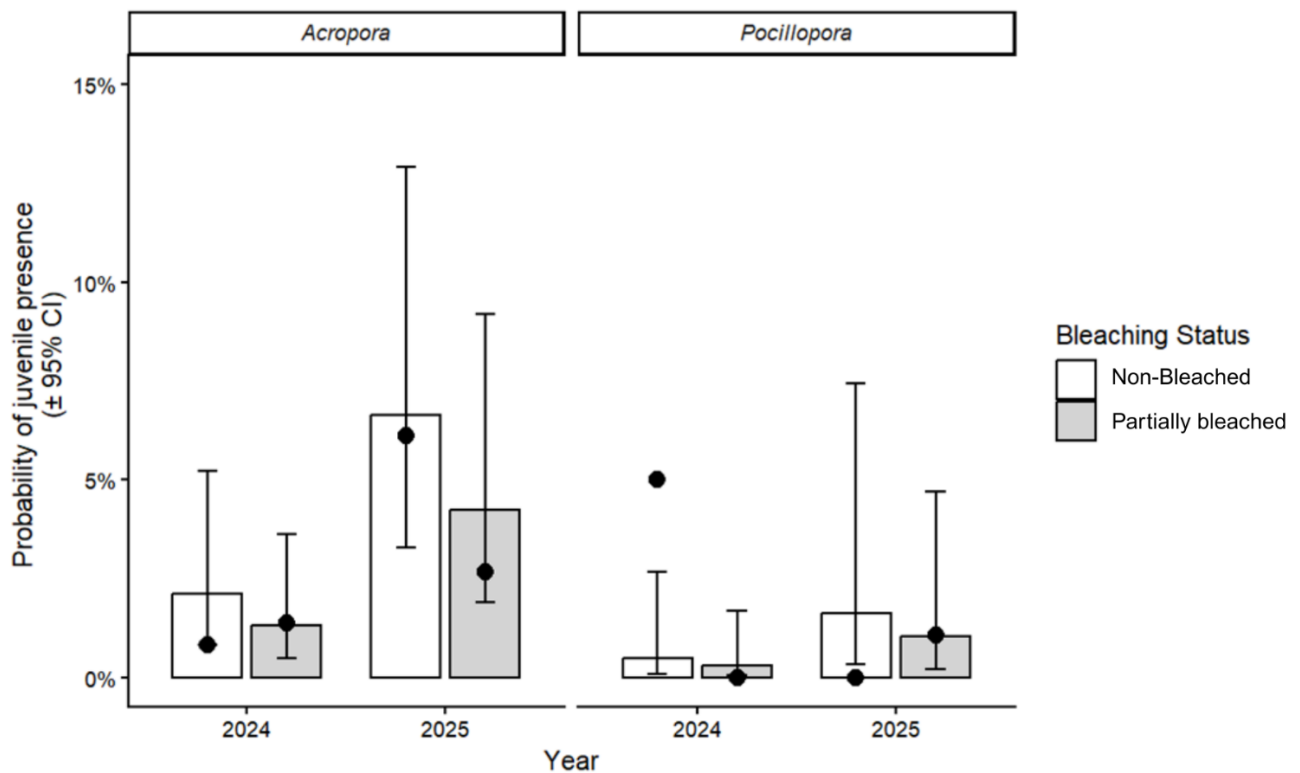


Figure 9. The predicted probability of juvenile *C. octofasciatus* presence within branching coral colonies by year (2024, 2025), coral genus (*Acropora*, *Pocillopora*) and bleaching status (non-bleached, partially bleached). Bars represent predicted probabilities derived from a binomial GLMM; error bars indicate the 95% confidence intervals; black dots represent observed proportions of colonies with juveniles present.

4. Discussion

This study investigated the ecological consequences of coral bleaching on *C. octofasciatus* populations on Koh Phangan's coral reefs between 2023 and 2025. Despite stable bleaching prevalence during peak bleaching months over the study period, *C. octofasciatus* population biomass and adult abundance declined, while juvenile abundance showed no significant variation. The low rate of colony occupancy by juveniles and complete absence of juveniles from fully bleached colonies highlights the narrow settlement requirements of this species and potential vulnerability to continued coral degradation.

Although bleaching prevalence did not significantly differ across the study period, bleaching remained present and consistently elevated throughout, likely reflecting the accumulated effects of thermal stress from the 2023-2025 El Niño event (Claar *et al.*, 2018). This pattern is consistent with global observations, which show sea surface temperatures, bleaching extent and severity continue to rise irrespective of ENSO transitions (NOAA Coral Reef Watch, 2025b). Even after bleaching events subside, coral mortality may perpetuate. *Acropora* specifically exhibits high mortality rates post-bleaching (Sakai *et al.*, 2019; Speare *et al.*, 2022). Despite substantial coral loss reported in reefs across East Asia - 11% of hard corals lost in the last decade (Souter *et al.*, 2021) - those around Koh Phangan have previously exhibited indications of resilience. Stahl *et al.* (2023) documented a mean annual increase in live Scleractinian coral cover on Koh Phangan reefs of 2.2% from 2014 to 2022, driven by an increase in plating coral abundance. This apparent resilience contrasts with both widespread global declines and the findings of this study, suggesting that the 2023-2025 El Niño event substantially impacted bleaching extent and coral condition around Koh Phangan, particularly among branching corals.

Despite the absence of changes in bleaching prevalence, both *C. octofasciatus* biomass and adult abundance declined during the study period. Since biomass was estimated from total fish length, this reduction may reflect a shift in population size structure towards smaller individuals over time (Festo *et al.*, 2026). However, the strong parallel decline in adult abundance suggests that biomass loss is more likely driven by adult mortality. Mortality may arise from several factors, including coral bleaching, which reduces the quality and quantity of live corals. This leads to the nutritional stress, physiological deterioration and starvation of resident fish populations, while simultaneously increasing risk of predation and disease (Pratchett *et al.*, 2004; Pratchett *et al.*, 2006). The migration of individuals from bleached corals into more suitable habitats provides an alternative explanation for an observed decline in adult abundance. However, the availability of suitable

habitats is limited by heightened bleaching extent, consequently increasing the likelihood of competition and agonistic interactions given the territorial and specialised nature of *C. octofasciatus* (Boström-Einarsson *et al.*, 2014). This reduces the probability of successful migration, making local mortality a more probable driver of population decline (Festo *et al.*, 2026).

The stability of juvenile abundance across years could suggest resilience of the recruitment process to coral bleaching. The predicted probability of juvenile presence increased between 2024 and 2025, suggesting that while total juvenile counts remained statistically unchanged, spatial distribution and settlement patterns shifted across years. Recruitment is a resource-limited, spatially and temporally variable process that governs the densities of fish populations (Wilson *et al.*, 2013). This temporal change may therefore reflect increasing pressure on the diminishing pool of available high-quality settlement habitats rather than a genuine recovery in recruitment.

Together, stable juvenile counts alongside declining adult abundance may reflect a failure of recruited juveniles to survive the transition into the adult population. Accessibility of high-quality live coral is essential for the successful settlement of *C. octofasciatus* (Wilson *et al.*, 2013), therefore shifts in coral community composition and loss of live coral can lead to recruitment failure or elevated post-settlement mortality (Coker *et al.*, 2009; Boström-Einarsson *et al.*, 2014; Pratchett *et al.*, 2006).

Juvenile recruitment was rare overall, indicating the high degree of coral specificity characteristic of *C. octofasciatus* (Cole and Pratchett, 2013). Juveniles settled exclusively on branching *Acropora* and *Pocillopora* colonies, reflecting the narrow range of settlement habitats available to this species, consistent with previous findings by Taira *et al.* (2016) and Festo *et al.* (2026). Branching corals are particularly susceptible to bleaching (Speare *et al.*, 2022) and their abundance has declined around Koh Phangan in recent years (Stahl *et al.*, 2023). This disproportionate loss of

branching corals has likely limited recruitment opportunities for *C. octofasciatus* juveniles onto reefs, with implications for long-term population replenishment.

Within the pool of available branching corals, larger colonies were associated with higher juvenile abundance, indicating colony size strongly influences the capacity of corals to support juvenile *C. octofasciatus*. This relationship is ecologically intuitive: larger colonies provide a greater surface area, increased structural complexity, and more available refuge space, allowing them to accommodate a greater number of juvenile recruits (Fisher, 2023).

The probability of juvenile settlement did not differ significantly between non-bleached and partially bleached coral colonies, a pattern also reported by Festo *et al.* (2026), and remained consistent irrespective of coral colony size. This could indicate that partial bleaching does not compromise the coral's ability to support juvenile settlement. Large partially bleached colonies may retain sufficient patches of live tissue and structural refuge to provide food and shelter, thereby remaining viable habitats (Festo *et al.*, 2026). The absence of a significant difference in juvenile recruitment between bleaching states may suggest that juveniles are not actively selecting between non-bleached and partially bleached colonies. Alternatively, juveniles may be constrained by the declining availability of unbleached colonies and forced to settle opportunistically. However, previous studies demonstrate that juvenile *C. octofasciatus* and similar coral-dwelling species can exhibit preferences between coral bleaching states. Four stripe damselfish (*Dascyllus melanurus*), yellow-tail blue damselfish (*Chrysiptera parasema*) and *C. octofasciatus* have all been shown to prefer water conditioned by unbleached *Acropora* over water containing stressed or bleached corals (Coppock *et al.*, 2013). The observed association of juveniles and partially bleached corals, despite documented preferences for healthier hosts, may arise from the initial settlement of juveniles onto unbleached corals that subsequently bleached (Cole and Pratchett, 2011; Coppock *et al.*, 2013). Sensory cues, once reliable indicators of habitat quality, may have also become

progressively decoupled from actual habitat suitability with each disturbance event (McCormick *et al.*, 2010), potentially misinforming and trapping juveniles in sub-optimal habitats.

The absence of juveniles on fully bleached colonies could imply either active avoidance of fully bleached colonies or settlement failure shortly after recruitment occurs. Juveniles settling on fully bleached colonies may experience rapid mortality (Coker *et al.*, 2009) or migrate to nearby suitable colonies, potentially explaining their absence at time of sampling. Settlement onto fully bleached colonies incurs increased predation risk associated with higher visibility and reduced structural complexity (Coker *et al.*, 2009), as well as increased nutritional stress from the reduced quality of bleached coral tissue (Cole *et al.*, 2014). Inhabiting fully bleached colonies likely has severe survival consequences for juvenile *C. octofasciatus* as relocation may not be possible if food resources or habitat quality continue to deteriorate (Cole and Pratchett, 2011; Festo *et al.*, 2026). This is supported by Pratchett *et al.* (2004) who demonstrated that the body condition of redfin butterflyfish (*Chaetodon lunulatus*) deteriorated with increased coral bleaching. Comparable patterns have been observed in other coral-dwelling fish, such as lemon damselfish (*Pomacentrus moluccensis*) and humbug damselfish (*Dascyllus aruanus*), which rarely occupy bleached coral hosts (Coker *et al.*, 2009), supporting the conclusion that bleaching fundamentally compromises habitat suitability for coral-dependent juveniles.

This study detected declines in overall population biomass and adult abundance following the 2023-2025 mass bleaching event. Previous research suggests that demographic responses of corallivorous chaetodontids to bleaching are not always immediate, with population-level effects taking years to manifest following a bleaching event (Pratchett *et al.*, 2006). This lagged response likely reflects the gradual deterioration of food resources, habitat quality, and coral structure following bleaching. Nevertheless, a strong positive relationship between fish abundance and live coral cover is well established (Wilson *et al.*, 2013; Van Nguyen *et al.*, 2024). More specifically, *C.*

octofasciatus abundance has been positively correlated with Scleractinian coral cover across multiple regions where they are abundant including Indonesia, Malaysia, French Polynesia, Philippines and the Red Sea (Madduppa *et al.*, 2014). Collectively, these findings suggest that sustained declines in live coral cover drive reductions in the abundance and biomass of coral-dependent butterflyfishes.

Given the close associations between *C. octofasciatus* and live coral cover, demonstrated in this study and corroborated by previous research, population trends of this species may reliably reflect broader reef condition, making them a practical indicator for long-term reef monitoring. However, as a genus, butterflyfish responses to coral loss can be complex, delayed and highly species-specific (Cole and Pratchett, 2013), meaning findings for *C. octofasciatus* may not be generalisable to other species. Some butterflyfish species may exhibit behavioural or dietary flexibility, allowing them to persist temporarily despite deteriorating coral habitats, while others, such as *C. octofasciatus*, are more sensitive (Crosby *et al.*, 2013). The recovery patterns of butterflyfish are likely to mirror those of their associated coral species (Wilson *et al.*, 2013), and while coral assemblages can recover rapidly when coral recruitment is high (Wilson *et al.*, 2013), it remains unclear whether butterflyfish populations can recover on comparable timescales (Pratchett *et al.*, 2013).

As severity and frequency of bleaching events increase, fish larvae are increasingly exposed to bleached coral at settlement and may be forced to recruit onto less-suitable habitats or adapt towards greater dietary and settlement flexibility (McCormick *et al.*, 2010). Nevertheless, it is important to recognise that coral bleaching is only one component of the broader multifactorial pressures imposed by global climate change (Festo *et al.*, 2026). As such, correlations between bleaching trends and those observed in *C. octofasciatus* populations cannot be interpreted as causation. Thermal stress and altered water chemistry may themselves exert pressures on the abundance, distribution and resilience of fish populations (Wilson *et al.*, 2013).

This study provides a foundation for continued longitudinal monitoring of *C. octofasciatus* abundance and recruitment across a greater number of reef sites, enabling larger sample sizes and broader contextualisation of population trends at a regional scale. This would improve statistical power and generate baseline data currently lacking for this species, strengthening its case as a bioindicator. Moreover, coral bleaching is not inherently binary; partial bleaching spans a continuum of severity between unbleached and fully bleached states. Measuring and modelling bleaching as a continuous variable may reveal subtle differences in habitat suitability and juvenile recruit preferences, consistent with patterns identified in the literature, and improve our ability to detect early warning signals of reef deterioration.

This study provides evidence for declines in *C. octofasciatus* population biomass and adult abundance across the reefs of Koh Phangan between 2023 and 2025 despite stable bleaching prevalence. The complete absence of juveniles from fully bleached colonies, combined with their strong dependence on branching *Acropora* for settlement, highlights the particular vulnerability of this species to continued loss of structurally complex unbleached coral. These findings add to a growing body of evidence linking corallivorous butterflyfish populations to coral reef condition and support the potential use of *C. octofasciatus* as a bioindicator. Given the accelerating pace of coral bleaching, investment in understanding its impacts through detailed species-level monitoring has never been more vital.

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Appendices

Appendix Table 1. Model selection table for all response variables.

Response variable	Model terms	AIC	ΔAIC
Percent bleached	Year + (1 Survey date)	-457.1941	0.00
	Year	-114.8922	342.3019
	Year + (1 Reef site)	-114.1906	343.0035
	Year + (1 Reef site) + (1 Survey date)	-455.1941	2.00
Biomass	Year	2283.127	0.00
	Year + (1 Reef site)	2283.456	0.329

	Year + (1 Survey date)	-	-
	Year + (1 Reef site) + (1 Survey date)	-	-
Abundance	Year × Life stage	1974.501	0.00
	Year	2371.278	396.777
	Year × Life stage + (1 Reef site)	1976.501	2.00
	Year × Life stage + (1 Survey date)	-	-
	Year × Life stage + (1 Reef site) + (1 Survey date)	-	-
Juvenile count per colony	Colony size × Bleach status	150.371	0.00
	Colony size	147.758	-2.613
	Bleach status	169.560	19.189
	Colony size × Bleach status + (1 Reef site)	152.070	1.698
	Colony size × Bleach status + (1 Survey date)	-	-
	Colony size × Bleach status + (1 Reef site) + (1 Survey date)	-	-
Juvenile presence	Year + Genus + Bleach status + (1 Reef site)	357.697	0.00
	Year	364.604	6.902
	Genus	374.629	16.932
	Bleach status	373.534	15.837
	Year + Genus	362.206	4.509
	Year + Bleach status	363.047	5.350
	Genus + Bleach status	373.541	15.844

Year + Genus + Bleach status	361.557	3.860
Year + Genus + Bleach status + (1 Survey date)	359.133	1.436
Year + Genus + Bleach status + (1 Reef site) + (1 Survey date)	359.689	1.992

Note: Δ AIC calculated relative to the best fitting model for each response variable. Models with convergence failures are indicated by (-). **Bold** indicates the selected model.

Appendix Table 2a. Tukey-adjusted pairwise comparisons of bleaching prevalence between years, derived from a beta GLMM.

Contrast	z	p
2023 vs 2024	0.559	0.8419
2023 vs 2025	0.215	0.9747
2024 vs 2025	0.366	0.9287

Bold p-values indicate statistical significance ($p < 0.05$). * $p < 0.05$, *** $p < 0.001$.

Appendix Table 2b. Tukey-adjusted pairwise comparisons of total *C. octofasciatus* biomass between years, derived from a Gaussian GLMM.

Contrast	z	p	
2023 vs 2024	2.552	0.031	*
2023 vs 2025	9.746	<0.001	***
2024 vs 2025	6.622	<0.001	***

Bold p-values indicate statistical significance ($p < 0.05$). * $p < 0.05$, *** $p < 0.001$.

Appendix Table 2c. Tukey-adjusted pairwise comparisons of *C. octofasciatus* abundance between years by life stage (adult, juvenile), derived from a negative binomial GLMM.

Life stage	Contrast	z	p
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Adult	2023 vs 2024	1.527	0.278	
	2023 vs 2025	7.210	<0.001	***
	2024 vs 2025	5.334	<0.001	***
Juvenile	2023 vs 2024	1.625	0.235	
	2023 vs 2025	1.683	0.212	
	2024 vs 2025	0.498	0.872	

Bold p-values indicate statistical significance ($p < 0.05$). * $p < 0.05$, *** $p < 0.001$.

Appendix Table 3. The number of branching coral colonies for each genus (*Acropora*, *Pocillopora*) and bleach status (non-bleached, partially bleached) sampled overall and those with juvenile *C. octofasciatus* present. Percentage occupancy (%) calculated as: (number of colonies with juveniles / total number of colonies) $\times$ 100.

Year	Genus	Bleach status	Colonies with juveniles	Total colonies	Occupancy (%)
2024	<i>Acropora</i>	Non-bleached	3	367	0.82
2024	<i>Acropora</i>	Partially bleached	5	360	1.39
2024	<i>Pocillopora</i>	Non-bleached	1	20	5.00
2024	<i>Pocillopora</i>	Partially bleached	0	36	0.00
2025	<i>Acropora</i>	Non-bleached	22	359	6.13
2025	<i>Acropora</i>	Partially bleached	8	300	2.67
2025	<i>Pocillopora</i>	Non-bleached	0	47	0.00
2025	<i>Pocillopora</i>	Partially bleached	1	94	1.06