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Cumulative impact from disturbances drives hard coral loss and *Chaetodon* butterflyfish decline in Nha Trang Bay Marine Protected Area, Vietnam

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ABSTRACT

Loss of live hard coral cover often drives declines in reef fish abundance, particularly among obligate corallivores such as butterflyfishes (Family Chaetodontidae). In this study, we investigated the variations in hard coral cover and *Chaetodon* butterflyfish densities within the Nha Trang Bay Marine Protected Area (MPA), Vietnam, spanning nearly two decades (2005–2023). We monitored hard coral cover and butterflyfish densities at 5-year intervals from 2005 to 2015, then increased the monitoring frequency thereafter, and found that live hard coral cover plummeted by 25.8% across the entire study period. This habitat degradation directly mirrored changes in the butterflyfish assemblages. Between 2005 and 2018, both post-recruit (1.1–5.0 individuals/100 m²) and recruit (0.1–1.6 individuals/100 m²) densities remained stable. However, both cohorts suffered sharp declines through 2023. We attribute this collapse to cumulative acute disturbances, including two major typhoons (Damrey in November 2017 and Rai in December 2021), a mass coral bleaching event, and a crown-of-thorns starfish outbreak in 2019. Crucially, we detected no signs of coral or fish recovery following these impacts, even within the strictly protected core zones (NWMU and SWMU) of Mun Island.

Keywords: Butterflyfishes, disturbance, coral loss, coral bleaching, COTS.

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Introduction

Severe or cumulative disturbances that drive extensive coral loss severely disrupt reef fish assemblages [1–5]. Most critically, acute coral mortality triggers rapid declines in the abundance and diversity of coral-dependent species, notably coral-feeding butterflyfishes (family Chaetodontidae). Even for species without direct dietary reliance on live corals as adults, loss of coral cover restricts larval settlement and recruitment [6], ultimately depressing overall reef fish richness and diversity [7]. For instance, an 8-year study in Papua New Guinea revealed that a 50% reduction in coral cover drove down species richness across more than 75% of reef fishes, even within marine reserves [8].

Butterflyfishes serve as prime models in coral reef ecology [9] due to their strict dependence on live hard corals [4, 10, 11]. This reliance is most pronounced in obligate corallivores [12, 13], which require live tissue both for nutrition and as critical settlement habitat [11, 14]. Specifically, multiple obligate *Chaetodon* species preferentially rely on branching, tabular, and corymbose *Acropora* corals [5, 7, 15]. While *Chaetodon* recruits exhibit high spatio-temporal variability [16, 17] - which conspecific density [18], predator pressure [19], post-settlement survival [20], and microhabitat structure [11, 13, 21] modulate - finely branched corals remain essential year-round settlement sinks across the Indo-Pacific [11, 21, 22]. Consequently, researchers globally deploy the genus *Chaetodon* as a bioindicator of coral reef health [23, 24]. Yet, while environmental impacts clearly deplete adult populations [25, 26], we still lack studies quantifying the proportional decline of adult densities relative to recruitment pulses. This knowledge gap stems partly from a biphasic life cycle and highly dispersive larval phase [11], which decouple local recruitment from local adult stock in favor of regional larval supply [27, 28]. Additionally, intense post-settlement density-dependent mortality [29] combined with ontogenetic habitat shifts [11] further obscures any direct proportional link between adult and recruit densities.

To address these dynamics, we focused our study on the Nha Trang Bay MPA, which encompasses 249.65 km² from Mui Ke Ga to Cu Hin Cape. This region supports exceptional biodiversity and critical coral reef ecosystems that anchor the ecological and economic development strategies of Khanh Hoa province [30, 31]. Recent comprehensive assessments confirm that this biodiversity hotspot hosts higher coral and reef fish richness than many global counterparts, ranking it among the richest marine sites in Vietnam [31]. Despite its ecological value, chronic overexploitation, destructive fishing, sedimentation, crown-of-thorns starfish (COTS; *Acanthaster planci*) outbreaks, coral bleaching, and mass tourism have driven severe benthic degradation [30, 32–35], particularly stripping out dominant hard corals like *Acropora* and *Montipora* [34, 35].

Over the past decade, a barrage of acute natural and anthropogenic shocks has hammered the MPA, including mass bleaching events (2010, 2019) [31, 32, 36], severe COTS outbreaks (2002, 2019) [30–32, 35], and two catastrophic tropical storms: Typhoon Damrey (November 2017) and Typhoon Rai (December 2021). Because no study has yet quantified the cumulative biodiversity loss from these compounding pressures, we analyzed the long-term temporal trends of live coral cover alongside corresponding butterflyfish densities. By integrating these interdependent metrics, we establish a robust proxy to evaluate how cumulative disturbances reshape local fish communities. Ultimately, we leverage these findings to propose targeted management frameworks designed to accelerate the resilience and recovery of reef resources across Nha Trang Bay.

Materials and methods

Data sources and collection

Although the Institute of Oceanography conducted numerous research initiatives, mandates, and projects on the coral reef ecosystems of Nha Trang Bay MPA between 2005 and 2023, divergent study objectives and sampling scales led to spatial and temporal

inconsistencies, particularly in the reef fish datasets. To resolve these discrepancies, we selectively compiled data from identical, representative reef sites that we sampled exclusively between June and August across all survey years. This approach synchronized the seasonal window and established a uniform spatio-temporal framework for robust ecological assessment.

From this standardized dataset, we filtered six reef sites with continuous data coverage: (1) Vung Island (HVUN), (2) Bai Bang (BBAN), (3) Northwest Mun Island (NWMU), (4) Southwest Mun Island (SWMU), (5) Southeast Tam Island (SETA), and (6) Northeast Mieu Island (NEMI) (Fig. 1). Our monitoring timeline tracked these sites at strict five-year intervals from 2005 to 2015 (2005, 2010, 2015), before shifting to

high-frequency annual or biennial assessments during the disturbance-heavy 2017–2023 window (2017, 2018, 2019, 2020, and 2023) to capture the impacts of two major typhoons, widespread coral bleaching, and COTS outbreaks. These sites represent contrasting enforcement regimes. The Nha Trang Bay Management Authority strictly protects and enforces no-take regulations at NWMU and SWMU on Mun Island. Conversely, although local authorities designated HVUN (Vung Island and Cau Island) as restricted zones in 2001, the Khanh Hoa Salanganes Nest Company manages the terrestrial islands primarily for bird nest harvesting; because this leaves the surrounding waters and coral reefs exposed to fishing pressures, we do not classify these latter sites as strictly protected areas.

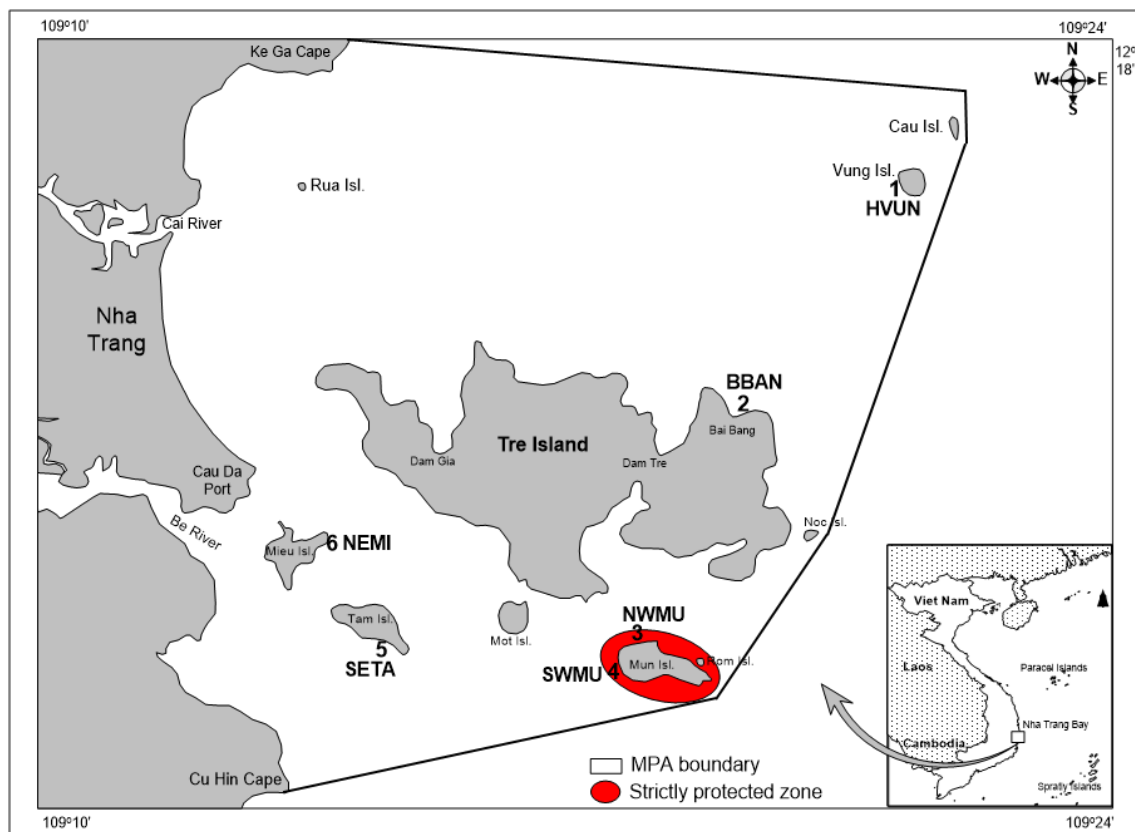


Figure 1. Permanent study sites of coral reefs in Nha Trang Bay MPA from 2005 to 2023. The frame is the boundary of the MPA

At each reef site, we conducted sampling across two depth strata: the reef flat (~ 2–4 m

depth) and the reef slope (5–8 m depth). Within each stratum, we deployed four 20-meter

replicate transects, maintaining a 5 m interval between adjacent transects in accordance with the ReefCheck protocol [37]. Approximately 10–15 minutes after transect deployment to allow fish behavior to normalize, observers performed slow underwater swims along the lines to census butterflyfishes. We grouped the observed fish into two main taxonomic categories: *Chaetodon/Parachaetodon* and *Chelmon/Coradion/Forcipiger/Hemitaenichthys/Heniichthys*. We further categorized individuals into two distinct size classes: “recruits” (≤ 4 cm total length, TL) [38–41] and “post-recruits” (> 4 cm TL, including juveniles to adults). Observers recorded all target fishes within a 5 m wide belt along each 20 m transect (2.5 m on either side of the centerline).

In parallel with the fish censuses, we quantified benthic cover across the six sites using the Point Intercept Transect (PIT) method. Along each 20-meter transect, we recorded the substratum type at 0.5-meter intervals [37]. The recorded benthic categories comprised live hard corals (including hydrozoan *Millepora* and octocorals *Heliopora* and *Tubipora*), soft corals, recently killed corals, sponges, turf algae, coralline algae, fleshy macroalgae, coral rubble, rock, sand, silt/clay, and others.

Data analysis

Because this study aimed to isolate the temporal responses of butterflyfishes to live coral loss, we restricted our downstream analysis exclusively to the obligate corallivores within the genus *Chaetodon*. For each site, we calculated the mean cover ($\pm$ standard error, SE) of live hard corals (HC) and soft corals (SC), alongside *Chaetodon* density, across the eight pooled 20 m transects per site. We standardized fish counts to individuals per 100 m² before analysis.

The Shapiro-Wilk test indicated that the raw datasets deviated significantly from normality. To satisfy the assumptions of analysis of variance (ANOVA), we log-transformed all density variables using $\log(x + 1)$ [15, 42] and transformed HC and SC cover data using the arcsine square-root method [38, 39, 42]. We visualized spatial and temporal variations in

coral cover and fish densities using boxplots. All statistical workflows ran in R (v4.4.1) [43], utilizing the tidyverse (v1.3.2) and ggplot2 (v3.4.4) packages for data manipulation and visualization, and vegan (v2.6-4) for multivariate operations. We constructed two-way ANOVA models to evaluate the main and interactive effects of reef site and survey year on coral cover and fish densities. We implemented these models using the emmeans package (v1.10.0) and applied Tukey’s post hoc adjustments for multiple pairwise comparisons.

Results and discussion

Temporal variation in coral covers

The pooled hard coral (HC) cover across the six representative reef sites remained statistically stable or showed only minor, non-significant fluctuations between 2005 and 2015, ranging from 29.8% to 34.6%. However, our data captured a subsequent, severe benthic collapse. Mean HC cover fell to $24.4\% \pm 2.6$ SE in 2017 and $17.5\% \pm 2.4$ SE in 2018, culminating in an absolute decline of 25.8% coral units by 2023, where cover reached an all-time low of $8.7\% \pm 2.1$ SE (Fig. 2). Two-way ANOVA confirmed that HC cover varied significantly across both sites and years ($df = 7$, $F = 18.05$, $p < 0.001$). Tukey’s post hoc tests verified that while the initial decline between 2005 and 2017 lacked statistical significance ($p > 0.05$), HC cover from the 2005–2017 baseline years differed profoundly from the degraded 2018–2023 period ($p < 0.01$ to 0.001), with the sole exception of the 2017–2018 transition. Notably, we detected no statistical variance between individual years within the 2018–2023 window ($p > 0.05$), indicating a sustained suppressed state. In stark contrast, soft coral (SC) cover remained consistently low throughout the study period, fluctuating minimally between 1.9% and 4.2% (Fig. 2) with no significant spatio-temporal variations (ANOVA, $df = 7$, $F = 0.97$, $p > 0.05$).

Site-specific evaluations revealed that while most locations exhibited structural degradation over time, the magnitude and trajectory of HC loss depended heavily on localized conditions

(Fig. 3). Two sites broke this general trend: HVUN consistently exhibited depauperate baselines with low, unchanging cover (2.5–6.8%, $p > 0.05$), while NEMI remained exceptionally resilient, maintaining stable cover between 26.3 and 33.3% ($p > 0.05$), despite a transient localized drop to 13.4–16.6% during 2019–2020. Conversely, the remaining four sites suffered significant, acute coral mortality ($p < 0.01$). At BBAN, HC cover dropped significantly between the historical baseline

(2005–2015) and the post-2017 period ($p < 0.01$). At SETA, significant structural shifts occurred between 2005 and 2010, and again between 2010 and the collapsed 2019–2023 window. Most remarkably, despite their status within the strictly protected no-take core zones, SWMU and NWMU experienced the most catastrophic structural collapses, with significant post hoc differences separating the 2005–2017 baseline years from the highly degraded 2018–2023 period.

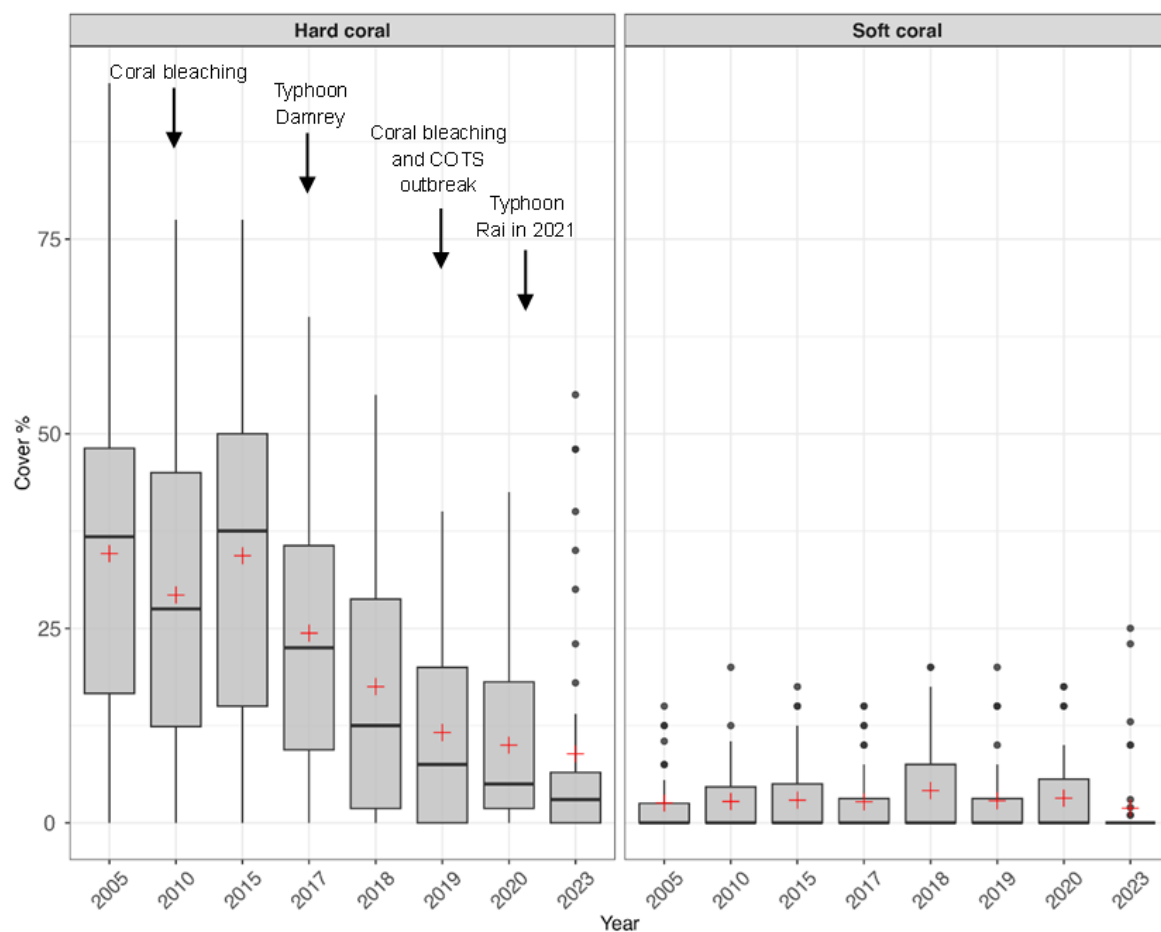


Figure 2. Temporal variation in overall covers of HC and SC in Nha Trang Bay MPA. The cross (+) within boxplots indicates the mean value, and the central line is the median value

The widespread collapse of HC cover in Nha Trang Bay - which began with a moderate decline in 2018 and escalated to severe loss by 2023 - demonstrates that these reef systems succumbed to compounding physical and biological threats. This footprint matches the

destructive sequence of Typhoon Damrey (Storm No. 12) in November 2017 and Typhoon Rai (Storm No. 9) in December 2021, which interacted with a mass coral bleaching event and an active COTS outbreak in 2019. While localized anthropogenic pressures such as

destructive fishing or terrestrial runoff could theoretically exacerbate this decline, we currently lack empirical data to substantiate their relative contributions.

Our timeline indicates that Typhoon Damrey exerted localized, restricted physical damage, leaving the broader bay-wide coral framework largely intact through early 2018. This moderate footprint contrasts sharply with the devastating impact of Typhoon Rai in December 2021. Typhoon Rai obliterated the benthic architecture across almost all monitoring stations, including the well-enforced, strictly protected marine reserves surrounding Mun Island. Hydrodynamic directionality and localized storm intensity during the 2018–2021 window explain why individual reef sites exhibited highly divergent

patterns of coral loss. Photographic evidence and citizen-science field reports compiled by local dive communities in June 2022 corroborate this widespread physical devastation. Furthermore, long-term datasets from the “Khanh Hoa Province Coral Reef Monitoring Program”, which the Institute of Oceanography executed, provide quantitative validation at the Mun Island stations (Fig. 4). Following Typhoon Damrey in late 2017, the reefs retained fair ecological health, with NWMU and SWMU supporting 26.6–30.6% HC cover and 0.3–13.1% SC cover. However, by August 2022 - eight months after Typhoon Rai - compounding storm damage had decimated these assemblages, plunging HC cover to a mere 1.9–9.7% and SC cover to 0.3–7.2% (Nguyen Van Long, unpublished data).

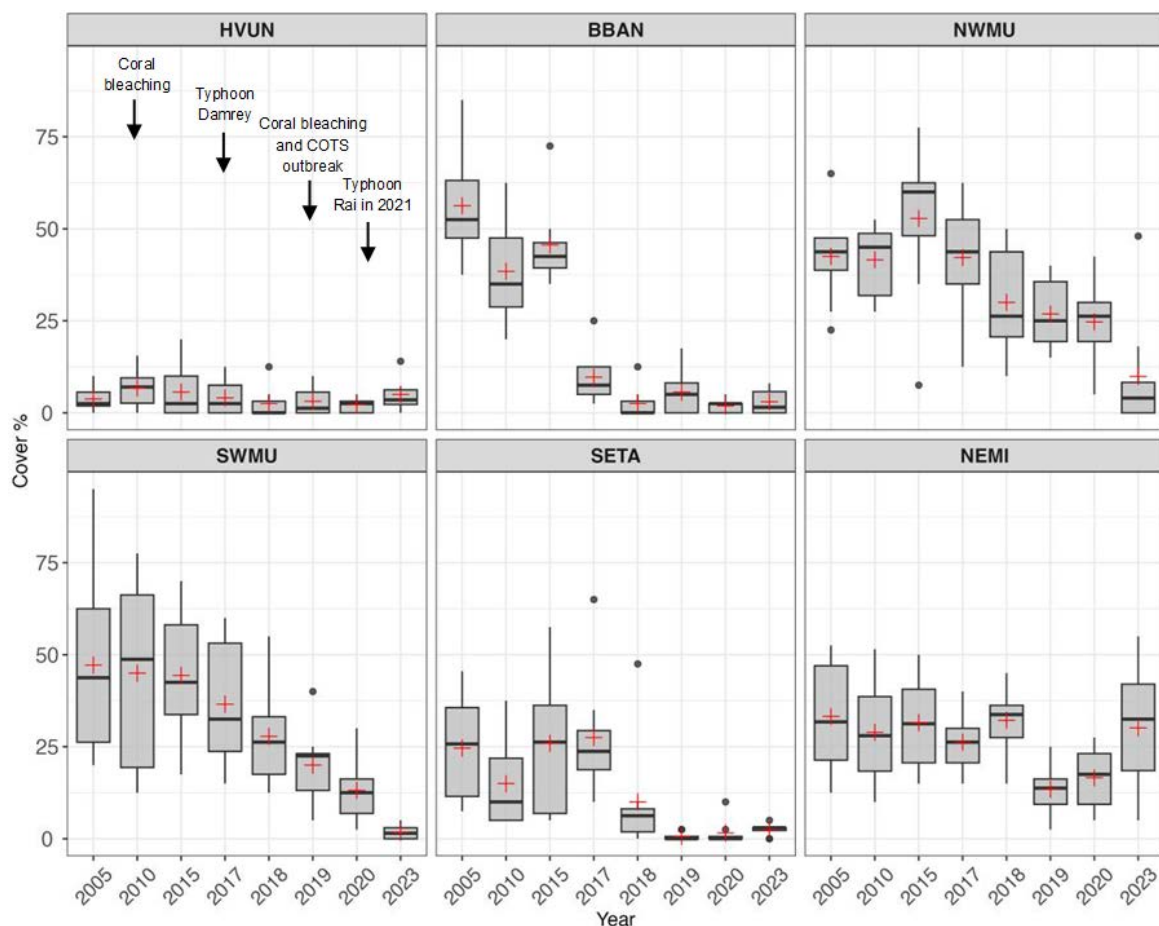


Figure 3. Temporal variation in mean cover of HC at reef sites. The cross (+) within boxplots indicates the mean value, and the central line is the median value

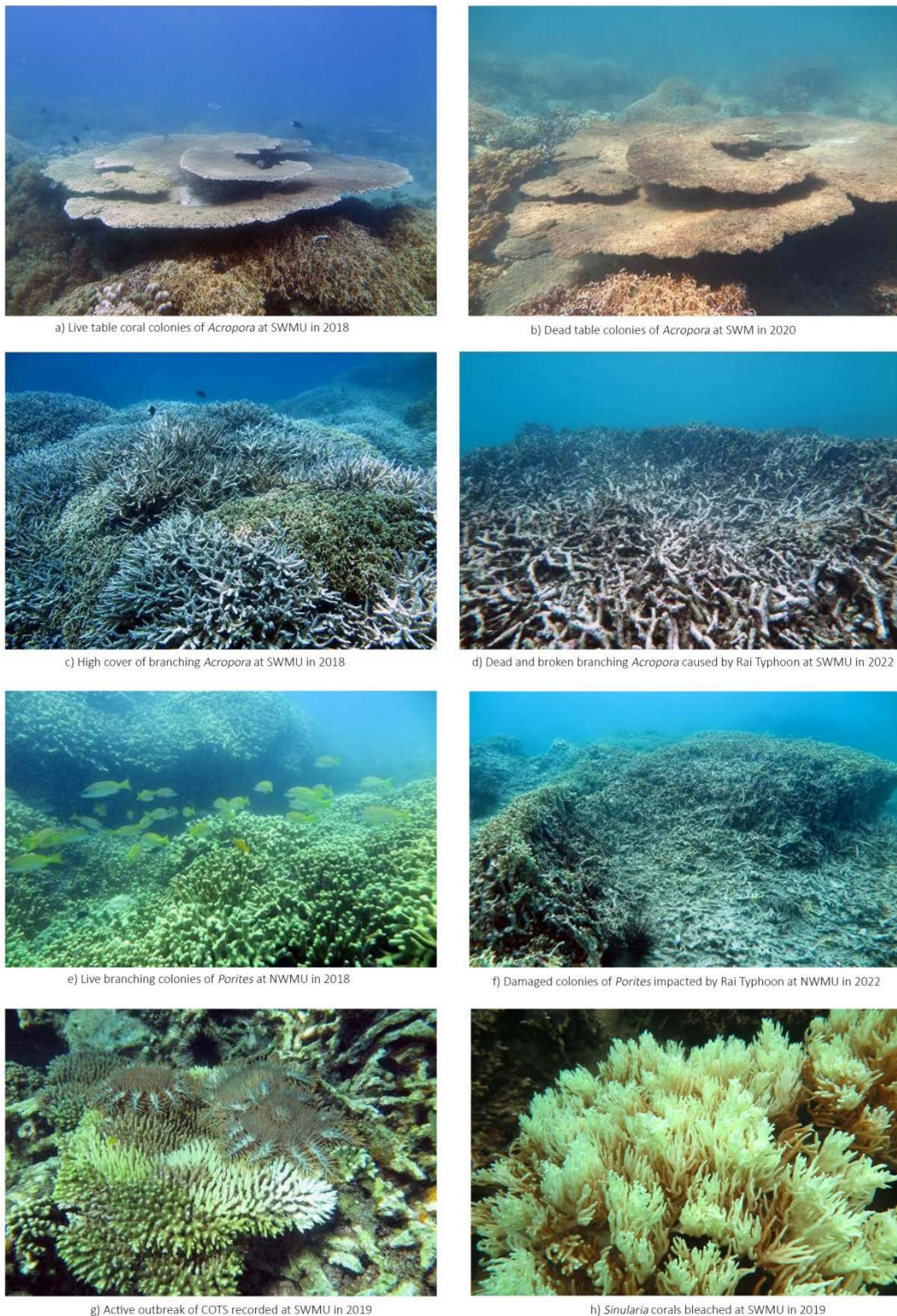


Figure 4. The condition of coral reef degradation within Mun Island in the restricted protected zone resulting from recent natural and anthropogenic disturbances

In addition to storm-induced mechanical destruction, a severe marine heatwave triggered a mass coral bleaching event during June–July 2019, affecting an average of 39.5% of the remaining HC cover. This bleaching prevalence exceeded concurrent levels recorded at other prominent Vietnamese reef systems, including Nui Chua, Con Dao, and Phu Quoc [36]. Compounding this thermal stress, a severe COTS outbreak plagued the MPA between 2017 and 2019, driving mean COTS densities above 2 individuals/100 m² - double the densities that researchers recorded at Nui Chua and Con Dao during the same period [31]. COTS populations peaked in 2019 at 4.2 individuals/100 m², representing a 2.4-fold amplification over 2013–2014 baselines [35]. Because an individual starfish can consume 5–17 m² of live coral tissue annually at outbreak thresholds (≥ 1 individual/100 m²), this high population density drove widespread coral mortality [44–46]. Previous demographic models suggest that when COTS outbreaks strip out over 90% of structural hard corals, full benthic recovery can require anywhere from 9 to 100 years, depending on regional larval connectivity [49].

Temporal variation in the density of butterflyfishes

We recorded a total of 1,634 *Chaetodon* butterflyfishes across the eight survey years, comprising 321 recruits (≤ 4 cm TL) and 1,313 post-recruits (> 4 cm TL). The strictly protected marine reserves at NWMU and SWMU supported the highest carrying capacities, hosting 434–555 individuals per site - a 2.1 to 4.2 fold inflation compared to the degraded or partially protected habitats of HVUN, BBAN, SETA, and NEMI (133–203 individuals).

Mean *Chaetodon* post-recruit density across the MPA fluctuated between 1.1 and 5.0 individuals/100 m² over the 18-year timeline. Post-recruits declined slightly from 5.0 individuals/100 m² in 2005 to 3.9 individuals/100 m² in 2010, before stabilizing through 2018 (3.8–4.3 individuals/100 m²). However, we detected an abrupt, rapid population collapse after 2018: post-recruit densities fell to 2.4 individuals/100 m² by 2020

and reached a historic low of 1.1 individuals/100 m² by 2023 (Fig. 5). Recruit densities also showed similar suppression, ranging from 0.1 to 1.6 individuals/100 m². While recruit counts fluctuated historically, the overarching baseline remained stable from 2005 to 2017, initiated a minor downturn in 2018 (0.9 individuals/100 m²), and collapsed sharply by 2023 to a mean of 0.2 individuals/100 m² (Fig. 5). Two-way ANOVA confirmed that both post-recruit (df = 35, $F = 4.087$, $p < 0.001$) and recruit (df = 35, $F = 3.952$, $p < 0.001$) cohorts experienced significant, bay-wide population declines over time, concentrated primarily within the 2018–2023 window.

At the individual site level, post-recruit cohorts exhibited highly divergent trajectories. At BBAN, NWMU, SWMU, and SETA, densities remained statistically invariant between 2005 and 2018 ($p > 0.05$) before undergoing sharp, significant post-2019 collapses ($p < 0.05$) (Fig. 6). Conversely, HVUN and NEMI maintained stable or marginally increasing adult densities throughout the disturbance window ($p > 0.05$). The strictly protected core zones (NWMU and SWMU), which initially supported high baseline carrying capacities, showed the most pronounced, statistically clear downward trajectories. In contrast, the degraded or unprotected sites (HVUN and NEMI) exhibited only sporadic, isolated inter-annual variations.

Recruit cohorts displayed highly synchronized trajectories across almost all monitoring sites, remaining stable from 2005 to 2017 ($p > 0.05$) before undergoing significant, uniform declines between 2018 and 2023 ($p < 0.01$) (Fig. 7). This temporal decoupling indicates that recruitment failure began immediately after Typhoon Damrey in 2017. In contrast, adult and post-recruit populations resisted immediate shifts, declining only after compounding biological shocks emerged in 2019. Pairwise comparisons confirmed a fundamental demographic shift separating the historical baseline era (2005–2017) from the contemporary collapsed era (2018–2023) across the majority of sites, while intra-period variations remained statistically negligible.

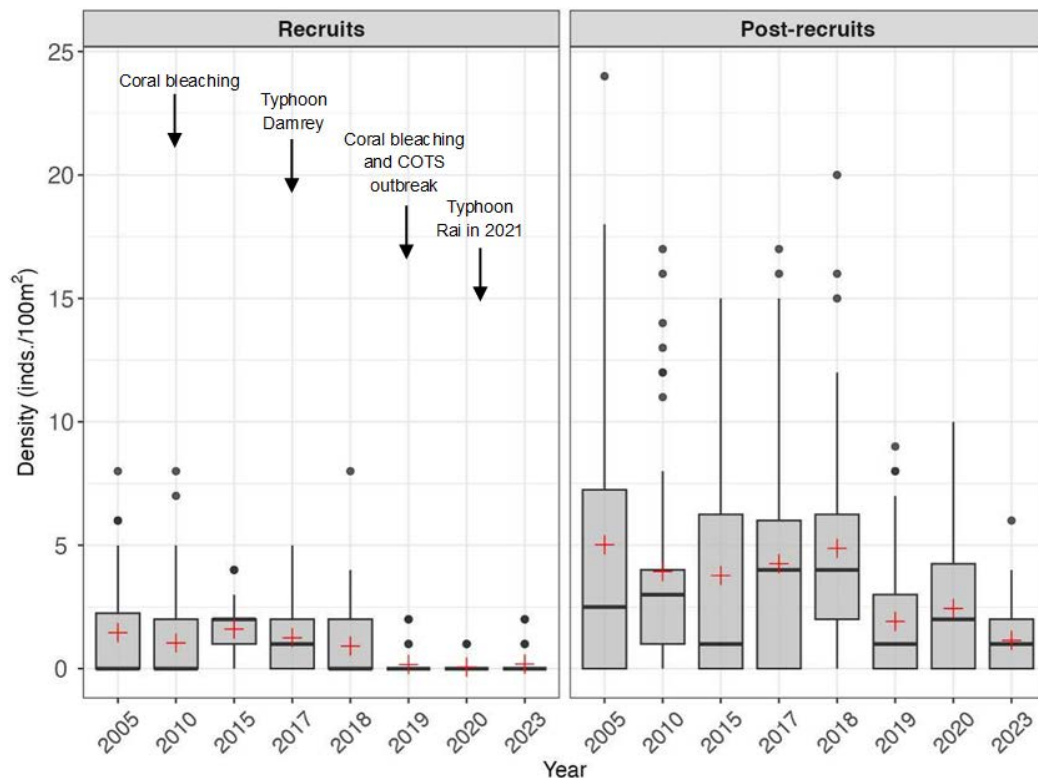


Figure 5. Temporal variation in mean density of *Chaetodon* post-recruits and recruits. The cross (+) within boxplots indicates the mean value, and the central line is the median value

The temporal stability of both post-recruit and recruit densities through early 2018 indicates that the localized, moderate hard coral loss that Typhoon Damrey inflicted did not trigger an immediate demographic collapse within the *Chaetodon* assemblage. Conversely, the catastrophic, sustained decline in butterflyfish densities from 2019 onward directly mirrors the widespread loss of hard coral architecture caused by Typhoon Rai and the 2019 biological disturbances. This tight coupling underscores the direct dependence of corallivorous reef fish on complex benthic habitats. Multiple lines of evidence confirm that obligate *Chaetodon* species are highly sensitive to loss of live hard coral, particularly branching, tabular, and encrusting morphospecies that provide both primary diet and structural refuge [14, 48]. Because juvenile *Chaetodon* rely on complex live coral frameworks - especially *Acropora* - for post-settlement survival [5, 15, 49], the systemic loss of dominant *Acropora* and *Montipora* assemblages across Nha Trang Bay has undermined recruitment success

and fundamentally reorganized the broader reef fish community structure.

The simultaneous post-2018 collapse of both recruit and post-recruit cohorts highlights three potential recruitment dynamics operating within the MPA: (1) restricted self-recruitment, where local adult depletion directly limits local larval production; (2) external larval dependency, where local recruitment relies entirely on connectivity with external source reefs; and (3) structural habitat loss, where recruit settlement fails due to the loss of fine-scale branching coral architecture. If regional source reefs are suffering similar climate-driven degradation, regional larval supply declines, leading to widespread recruitment failure within the Nha Trang Bay MPA. Empirical tracking methods - including daily otolith increment analysis [50], tetracycline embryo tagging [51], and otolith microchemistry [52] - indicate that Indo-Pacific reef fishes typically display mixed recruitment strategies, balancing localized self-recruitment with regional open connectivity.

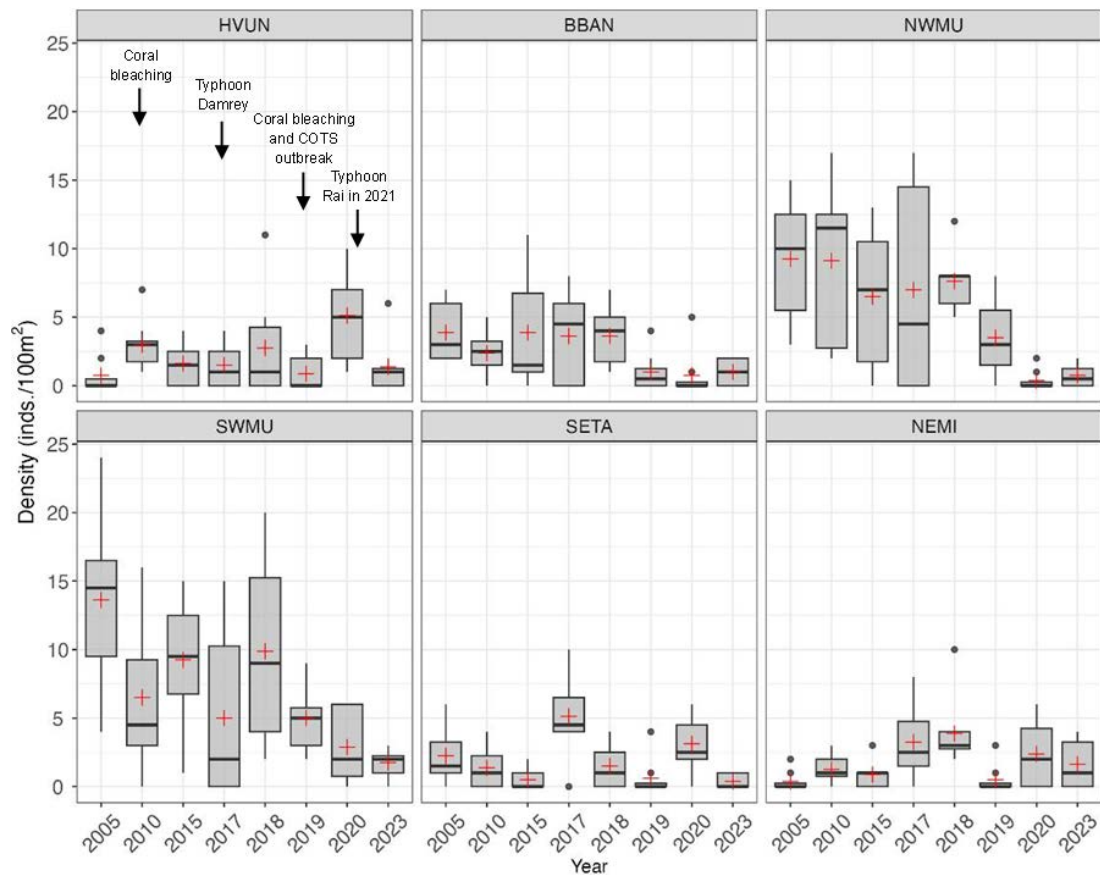


Figure 6. Temporal variation in the density of *Chaetodon* post-recruit at reef sites. The cross (+) within boxplots indicates the mean value, and the central line is the median value

In this study, adult post-recruit densities at HVUN and NEMI rose slightly between 2018 and 2023 despite severe environmental shocks, yet recruit counts at these exact sites plummeted. This divergence indicates that local self-recruitment is not the primary driver of replenishment. Instead, these systems appear heavily reliant on external larval inputs, though confirming this hypothesis requires further biophysical hydrodynamic modeling. The high spatial and temporal heterogeneity of *Chaetodon* recruitment across the bay indicates that complex interactions between hydrodynamic transport, biological interactions, and localized human stressors [53, 54] govern replenishment pathways. The dependence of recruitment success on both geographic position and the precise timing of regional oceanographic features remains a core tenet of reef fish ecology, a dynamic that our dataset clearly reflects.

Benthic recovery and the restoration of *Chaetodon* communities to pre-2017 baselines will likely require one to two decades of intensive, uninterrupted management. This projection aligns with global demographic models, which estimate a mean annual increase in coral cover of 2.4% during undisturbed recovery phases [55]. Crucially, our data show that marine reserve designation exerts negligible direct control over butterflyfish densities when detached from habitat quality; these specialist populations track benthic structural integrity rather than no-take enforcement metrics. While specialized *Chaetodon* assemblages can display remarkable structural stability across multi-decadal scales (up to 31 years) under moderate environmental fluctuations, the sharp asymmetry between their rapid collapse and protracted recovery rates exposes them to local extinction under escalating climate-driven disturbance regimes.

Consequently, we must implement targeted conservation and active restoration frameworks immediately. We recommend prioritizing the reef frameworks at Mun, Vung, and Northeast Mieu islands for enhanced enforcement, given their high baseline carrying capacities and structural recruitment potential. Within the strictly protected core zones of Mun and Rom islands, management authorities must enforce zero-

tolerance bans on resource extraction and further restrict marine tourism pressures. Finally, scaling up active coral restoration - specifically via macro-fragment transplantation and the deployment of sexually-derived larval seeding on degraded substrates - represents a critical intervention to accelerate the recovery of both the benthic habitat architecture and its dependent reef fish assemblages.

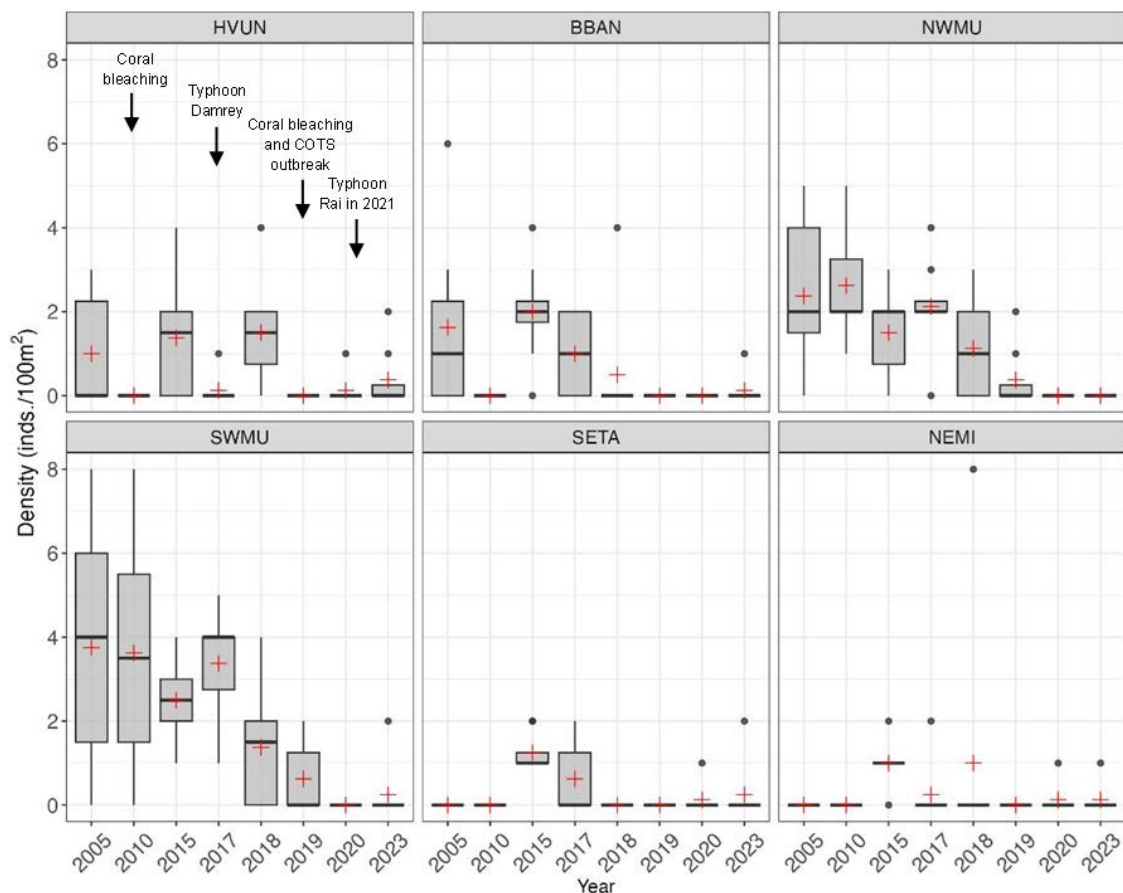


Figure 7. Temporal variation in the density of *Chaetodon* recruits at reef sites. The cross (+) within boxplots indicates the mean value, and the central line is the median value

Conclusion

Compounding natural and anthropogenic disturbances - principally Typhoons Damrey (2017) and Rai (2021), a mass bleaching event (2019), and severe COTS outbreaks (2019–2021) - have driven severe, systemic coral reef degradation across Nha Trang Bay MPA. This benthic collapse led to a rapid decline in hard

coral cover, triggering a synchronous collapse of *Chaetodon* butterflyfish populations between 2017 and 2023. Demographically, recruit densities collapsed immediately following the 2017 hurricane due to the loss of preferred branching microhabitats. In contrast, post-recruit adult populations exhibited a lagged response, crashing 1–2 years later under the compounding pressure of marine heatwaves

and COTS outbreaks. Given the current depauperate densities of adult broodstock and the bay-wide failure of larval recruitment, the recovery of these specialized butterflyfish assemblages and the broader coral reef ecosystem will be protracted, requiring at least a decade of strict, active marine conservation management.

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