

Near-term impacts of the 2024 mass coral bleaching event on benthic and fish communities in Okinawa Island, southern Japan

Lucas Yutaka Kimura

lucaskimura0924@gmail.com

University of the Ryukyus

Rickdane Gomez

University of the Ryukyus

Takashi Nakamura

University of the Ryukyus

Research Article

Keywords: thermal stress, bleaching impacts, coral communities, fish assemblages, subtropical coral reefs

Posted Date: July 20th, 2026

DOI: <https://doi.org/10.21203/rs.3.rs-7893239/v1>

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Additional Declarations: No competing interests reported.

Abstract

Mass bleaching events caused by elevated thermal stress continue to drive widespread degradation of coral reef ecosystems. In the summer of 2024, unprecedented thermal stress (18°C-weeks) in subtropical Okinawa Island, Japan, caused the most severe mass bleaching event recorded on record, coinciding with the Fourth Global Coral Bleaching Event. We assessed the near-term impacts of this event on benthic and fish communities across shallow (1–6 m) and deeper (8–15 m) zones at seven sites across Okinawa Island. Surveys were conducted before (March–April 2024), during (August 2024), and after (January–March 2025) the bleaching event. Bleaching was extensive ($69.8 \pm 3.2\%$), resulting in an average 46% decline in hard coral cover. Bleaching severity and coral mortality were strongly mediated by depth and influenced by site characteristics. Benthic shifts were evident, driven by high mortality of *Acropora* and the proliferation of algae on dead coral skeletons, while coral genera previously identified as thermally sensitive (e.g., *Pocillopora* and *Montipora*) showed resistance to bleaching. In contrast, short-term responses of fish communities were weak and limited to specific functional groups. Fish species richness and Shannon diversity remained stable despite coral loss, and only obligate corallivores showed declines in shallow reefs, whereas herbivores increased. These results provide the first integrated assessment of bleaching impacts on benthic and fish communities in Okinawa Island, highlighting depth-and taxon-specific coral vulnerability and the lagged nature of fish community responses. Sustained monitoring will remain essential to determine whether these patterns persist under continued warming.

1. Introduction

Mass bleaching events have become increasingly frequent and severe due to the rapid rise in sea temperatures driven by climate change (Hughes et al. 2018; Sully et al. 2019). Such events can lead to widespread coral mortality, resulting in substantial declines in live coral cover, the degradation of reef biodiversity, and the loss of ecosystem functions and services (McClanahan et al. 2002; Bell et al. 2013; Pratchett et al. 2014; Eddy et al. 2021). Prolonged coral loss also reduces the structural complexity of reef habitats, diminishing essential resources such as food, shelter, and settlement substrates for many reef-associated organisms (McClanahan et al. 2002; Pratchett et al. 2008). Reef fishes are integral to coral reef ecosystems, contributing not only to fisheries but also to key ecological processes (e.g., herbivory, predation, etc.) (Harborne et al. 2017; Brandl et al. 2019). Declines in functionally important fish taxa can undermine these processes and potentially drive phase shifts toward degraded or alternative reef states dominated by non-scleractinian taxa (Done 1992; Bellwood et al. 2006; Norström et al. 2009; Cruz et al. 2015). While traditional metrics of reef fish assemblages such as abundance, species richness, and biomass often show weak or inconsistent relationships with coral cover (Muruga et al. 2024), changes in these indicators and shifts in community composition following coral loss and structural collapse can have profound consequences for ecosystem functioning and resilience (Munday 2004; Bellwood et al. 2006; Wilson et al. 2006; Pratchett et al. 2011).

These dynamics are relevant in the Ryukyu Archipelago of Japan, where high marine biodiversity occurs despite the region's relatively high latitude (Hughes et al. 2002; Tittensor et al. 2010; Reimer et al. 2019). This diversity is driven mainly by the Kuroshio Current, which transports warm tropical waters and larval supply northward from the Philippines (Motomura and Matsunuma 2022). Okinawa Island, the largest island in the Ryukyu Archipelago, supports over 480 species of scleractinian corals (Kitano et al. 2020) and sustains highly diverse fish communities surpassing those of other regions along a similar latitude such as the northern Red Sea and the Persian Gulf (Parravicini et al. 2013; Barneche et al. 2019; Gomez et al. 2025a). As a subtropical reef system, Okinawa experiences large seasonal sea temperature variability (around 20–31°C; Singh et al. 2022), potentially driving distinct adaptations and community dynamics. Nonetheless, reefs around Okinawa have been increasingly threatened over the past three decades by typhoons (White et al. 2013; Kimura et al. 2024), coastal development and terrestrial runoff (Hongo and Yamano 2013; Masucci and Reimer 2019; Nakajima et al. 2025), and recurrent mass bleaching events (Yamazato 1999; van Woesik et al. 2011; Kayanne et al. 2017; Afzal et al. 2025).

Several major bleaching events have been recorded in Okinawa and the Ryukyus, including in 1980 (Yamazato 1999), 1998 (Fujioka 1999; Shibuno et al. 1999; Yamazato 1999; Sano 2004), 2001 (Strong et al. 2002); 2016–2017 (Kayanne et al. 2017; Masucci et al. 2019), and 2022 (Afzal et al. 2024, 2025) (Fig. 1b). Assessments of their impacts, however, have mostly been spatially limited and focusing only on benthic communities. Notably, the last studies to document bleaching-related fish community responses in the region date back to the 1998 global bleaching event (Shibuno et al. 1999; Sano 2004). Most recently, the 2024 bleaching event, corresponding with the Fourth Global Coral Bleaching Event (GCBE; Reimer et al. 2024), was the most severe on record in the region, with thermal stress reaching unprecedented levels. Here, we assessed the short-term impacts of the 2024 mass bleaching event on benthic and fish communities in Okinawa Island, Japan. In specific, we evaluated (1) the bleaching severity and changes in coral cover across sites and depth zones, (2) the shifts in benthic and coral genus composition across depth zones, and (3) the near-term changes in fish community metrics and abundance of different functional groups in response to coral loss. By documenting these impacts, our study contributes important site-level data from a warm subtropical reef system where impacts on fish communities have been underreported for more than two decades. Understanding the consequences of such an extreme bleaching event is essential for tracking reef trajectories and anticipating future ecosystem responses under accelerating climate stress.

2. Methodology

2.1 Study location and 2024 thermal stress event

This study was conducted at seven fringing reef sites in Okinawa Island, southern Japan (Fig. 1a). At each site, ten 20-m permanent transects were established at two depths: a shallow zone (reef flat to crest, 1–6 m) and a deeper zone (lower reef slope, 8–15 m) (Gomez et al. 2025a). Fish and benthic communities were surveyed before (March–April 2024) and after (Jan–Mar 2025) the bleaching event, with an additional benthic survey during peak bleaching (Aug 2024) at all sites except Nakijin.

From July–September 2024, Sea Surface Temperatures (SST) around Okinawa Island exceeded the local bleaching threshold (29.98°C), reaching an unprecedented peak Degree Heating Weeks (DHW) of 18°C-weeks in September—the highest on record for the island (Fig. 1b; Online Resource 1a). The DHW represents accumulated thermal stress, calculated as the number of weeks when SST exceeds the maximum monthly mean by $\geq 1^\circ\text{C}$, summed over a 12-week window (Liu et al. 2003). Thresholds of 4 and 8°C-weeks correspond to NOAA Bleaching Alert Levels 1 and 2, respectively, with the latter indicating widespread coral bleaching and some mortality (Kayanne 2017; Whitaker and DeCarlo 2024; Afzal et al. 2025). Temperature data were obtained from NOAA Coral Reef Watch Daily Global 5 km products, specified for Okinawa Island (longitude 127.5°–128.5°, latitude 26.0°–27.0°).

2.2 Benthic assessments

Benthic communities were surveyed along fixed transects across three time points at each site. Five 20-m permanent transects were established per depth zone to ensure spatial consistency. Benthic cover was recorded every 0.25 m along each transect using an underwater camera (Olympus TG-6), following the Point Intercept Transect (PIT) method (Hill and Wilkinson, 2004; Kimura et al. 2025). This produced 80 points per transect and a total of 400-point images per depth zone at each site. Photos of the underlying benthos were classified ex-situ into 11 major categories: hard coral, soft coral, other invertebrates, macroalgae, turf algae, coralline algae, cyanobacterial mat, dead coral with algae (DCA, or recently killed coral), bare rock, rubble, sand. Hard corals were identified to genus and assigned into one of ten morphologies: branching, corymbose, digitate, tabular, plate-like, phaceloid, foliose, encrusting, massive and solitary. Genus-level identification was aided by regional coral identification guides (Veron 1992; Nishihira and Veron 1995; Dai and Yourong 2020; Fukami et al. 2022) and taxonomic revisions were validated through the World Register of Marine Species (WoRMS; <https://www.marinespecies.org/>).

Bleaching severity for all hard and soft coral colonies on the transect points were classified into four categories following Frade et al. (2018): (1) No bleaching (no visible bleaching), (2) Partial bleaching (1–50% of colony affected), (3) Severe bleaching (51–100%), and (4) Recently dead (algal growth on colony visible). Bleaching prevalence was calculated as the proportion of bleached hard coral points (categories 2 and 3 combined) relative to all hard coral points on each transect. Five transects were treated as replicates, and mean values were used to characterize spatial patterns across depth zones and the entire Okinawa Island.

2.3 Fish community surveys

Fish communities were assessed using diver-based Underwater Visual Census (UVC) along the same transects as the benthic surveys, following Gomez et al. (2025a). Surveys were conducted between 10:00 and 16:00 to minimize diel variations in fish activity and community composition (Halford and Thompson 1994). All conspicuous, non-cryptobenthic fishes > 4 cm and observed within a 2.5 m belt on either side of the transect were recorded. Individuals were identified to species, counted, and estimated for total length (cm). Each transect was surveyed by a single diver to minimize disturbance and observer bias.

2.4 Data analyses

All statistical analyses were performed in RStudio version 4.5.1 (Posit Team 2025).

2.4.1 Benthic composition and bleaching prevalence

Effects of site and depth on bleaching severity of hard and soft corals were tested using cumulative link mixed models (CLMM; logit link) implemented in the *ordinal* package (Christensen 2025). Bleaching severity (levels 1–4) was treated as an ordinal response variable, with site and depth as fixed effects and transect as random effect. Post hoc pairwise contrasts were obtained using estimated marginal means calculated in the *emmeans* package (Lenth et al. 2025). Taxon-specific Bleaching Susceptibility Index (BSI) was calculated following McClanahan et al. (2004) and Dalton et al. (2020) and plotted against the percent change in coral cover for each taxon.

Changes in benthic cover (hard coral, soft coral, turf algae, DCA, macroalgae) were assessed using generalized linear mixed models (GLMMs; Beta family for hard coral and turf algae, zero-inflated Beta family for DCA, and Binomial family for soft coral and macroalgae) fitted using the *glmmTMB* package (Brooks et al. 2017). Model performance was evaluated with AIC and residual diagnostics from the DHARMA package (Hartig et al. 2024). Percentage cover was set as the response variable, with site and depth as fixed effects and transect as random effect. Pairwise contrasts between time points (pre- vs post-bleaching) were tested using the *emmeans* package (Lenth 2024).

Shifts in benthic composition and coral genera were visualized on Bray-Curtis matrices using a non-metric multidimensional scaling (NMDS) ordination in the *vegan* package (Oksanen et al. 2022). Ordinations were performed separately for each depth and significant variables driving observed differences were printed as arrow vectors using the *envfit* function in *vegan* (Oksanen et al. 2022). Temporal changes across sites and depths were tested using permutational multivariate analysis of variance (PERMANOVA) using *vegan* (Oksanen et al. 2022), and major benthic categories or coral genera contributing to dissimilarities were identified through similarity of percentages (SIMPER) analysis.

2.4.2 Fish metrics and composition

Information on each fish species, including taxonomy, diet, and trophic ecology, was compiled from FishBase (Froese and Pauly 2025) and published literature. Species were assigned to 10 intermediate functional groups modified from Pratchett et al. (2011), with corallivores classified following Cole et al. (2008) and herbivores following Green and Bellwood (2009).

Differences in fish species richness and Shannon diversity before and after bleaching were modeled with GLMMs. Species richness was fitted with a negative binomial distribution (log link) and Shannon diversity with a Gaussian distribution (identity link), both implemented in *glmmTMB* (Brooks et al. 2017). Fixed effects included time, site, and depth, with transects nested within sites as random effects. Fixed

effects were evaluated using likelihood ratio tests (LRT), and post hoc comparisons were derived with *emmeans* (Lenth 2024).

Changes in the abundance of intermediate functional groups following coral loss were modeled as the log response ratio (LRR) relative to percent change in coral cover. LRR was calculated as the natural log of the fold change in abundance after versus before bleaching:

$$LRR = \ln(A_{post} + 1 / A_{pre} + 1)$$

where *A* represents the mean abundance per transect. A constant was added to minimize skewed data and undefined results for zero data when log transformed. LRR values greater than 0 indicate increase in abundance relative to pre-bleaching levels, values less than zero indicate decline, and values close to zero indicate little or no change. Models for each functional group were tested using GLMMs (Gaussian, identity link), with LRR as the response variable, percent change in coral cover as the fixed effect and sites as random effects. Model coefficients were back-transformed to express percent change in abundance per 10% decline in coral cover. Additional tests were performed for the herbivore groups to investigate their responses to algal variables: macroalgae for browsers, and combined turf and DCA for grazer/detritivore, scrapers, and excavators.

Community-level changes by depth were visualized with NMDS on Hellinger-transformed Bray-Curtis matrices using *vegan* (Oksanen et al. 2022). Differences across survey time points were tested with PERMANOVA, while post-hoc pairwise comparisons were performed using the *pairwiseAdonis* package (Martinez Arbizu 2017). Species contributing to dissimilarities were identified using SIMPER.

3. Results

3.1 Bleaching rates and benthic shifts across sites and depth zones

The overall mean proportion of bleached hard corals was $69.8 \pm 3.2\%$ (mean $\pm$ standard error (SE)), with prevalence markedly higher in shallow zones ($81.1 \pm 2.31\%$) compared to deeper zones ($58.3 \pm 3.84\%$) (Fig. 2). The overall mean proportions of non-bleached and recently dead corals were $30.2 \pm 3.45\%$ and $8.57 \pm 3.17\%$, respectively (Fig. 2). Bleaching attenuation by depth was evident, as shallow zones at all sites exhibited higher bleaching prevalence than deeper zones (CLMM, $z = 7.07$, $p < 0.001$; Fig. 2). Bleaching of soft corals was also observed, with an overall bleaching prevalence of $59.5 \pm 7.4\%$, and higher rates in shallow zones ($94.5 \pm 2.65\%$) than deeper zones ($37.2 \pm 9.25\%$) (Online Resource 1b).

Overall, hard coral cover declined by nearly half following the bleaching event, from $46.2 \pm 2.6\%$ to $24.6 \pm 2.2\%$. This reduction was significant in both depth zones, with a more pronounced decline observed in shallow zones (*emmeans*, shallow: $p < 0.001$; deeper: $p = 0.006$) (Fig. 3). All sites showed significant declines in shallow zones ($p < 0.05$) (Fig. 3). In the deeper zone, significant reductions were observed only at Kakinouchi ($p < 0.001$) and Nakijin ($p = 0.003$), whereas the remaining deeper sites showed non-

significant changes (Fig. 3). Among sites, no significant changes in coral cover were detected at the east coast (Chinazaki ($p = 0.38$) and KGV ($p = 0.30$), whereas all other sites declined significantly ($p < 0.05$).

Soft coral cover mildly declined ($8.2 \pm 3.5\%$ to $7.0 \pm 3.7\%$; emmeans, $p = 0.040$) following observed fragmentation and tissue sloughing (Online Resource 1c). Turf algae cover increased slightly ($26.6 \pm 1.7\%$ to $29.2 \pm 2.1\%$) (emmeans, $p = 0.840$), and the cover of DCA increased greatly (0% to $17.6 \pm 2.5\%$) following bleaching (emmeans, $p < 0.001$), while macroalgal cover was more variable across sites but generally decreased ($5.8 \pm 1.5\%$ to $2.8 \pm 0.7\%$) (emmeans, $p = 0.461$) (Online Resource 1d).

Benthic community composition shifted significantly after bleaching in both depth zones (shallow: $pseudo-F = 15.40$, $p = 0.005$; deeper: $pseudo-F = 12.40$, $p = 0.005$). In the shallow zone, pre- and intra-bleaching communities were similar, while post-bleaching assemblages were distinct (Fig. 4a). This was driven by declines in hard coral cover ($p < 0.001$) and a corresponding increase in DCA ($p < 0.001$), as indicated by SIMPER analysis (Online Resource 2a). In the deeper zone, although the overall shift was less distinct (Fig. 4a), reductions in hard coral cover ($p = 0.024$) and consequent increases in DCA ($p < 0.001$) were also observed (Online Resource 2a).

3.2 Bleaching susceptibility and survival among hard coral genera

Scleractinian genera exhibited varying levels of bleaching susceptibility and subsequent changes in coral cover. *Acropora* was the only genus that showed both high bleaching susceptibility and substantial coral loss post-bleaching, highlighting its pronounced vulnerability to heat stress (Online Resource 1e). In contrast, genera such as *Pocillopora*, *Platygyra*, *Montipora*, *Dipsastraea*, and *Porites* displayed relatively low susceptibility and minimal declines in cover (Online Resource 1e), suggesting greater resistance to heat stress. *Favites* and *Goniastrea* exhibited high bleaching prevalence but low subsequent mortality, while *Cyphastrea* and *Merulina* showed relatively greater coral mortality despite low bleaching prevalence (Online Resource 1e).

Given these differences in bleaching susceptibility, the composition of hard coral genera shifted significantly in the shallow zones after bleaching ($pseudo-F = 7.31$, $p = 0.005$), whereas deeper zone communities remained intact ($pseudo-F = 7.31$, $p = 0.565$) (Fig. 4b). In the shallow zones, the shift in community composition was primarily driven by the decline in *Acropora* (SIMPER, $p = 0.001$) (Fig. 4b; Online Resource 2b).

3.3 Responses of fish assemblages to bleaching

Overall changes in fish species richness and Shannon diversity after bleaching were minimal and statistically non-significant (Species richness: $\chi^2 = 5.819$, $p = 0.668$; Shannon diversity: $\chi^2 = 8.494$, $p = 0.387$). Site-level trends varied, with the majority showing minute declines or negligible changes (Fig. 5). Only Kakinouchi exhibited consistent increases in both species richness and Shannon diversity across depth zones (Fig. 5).

Responses in the abundance of fish functional groups to coral loss were non-uniform. Most herbivore groups (browsers, grazer/detritivores, and excavators) tended to increase in abundance in shallow zones and declined in deeper zones as coral loss intensified, while piscivores showed the opposite trend (Fig. 6). Other groups exhibited modest declines or stable patterns (Fig. 6). Most of these relationships were weak, except for browsers, excavators, and obligate corallivores (Fig. 6). Furthermore, responses of these groups were depth zone-specific. For every 10% loss in coral cover, browser abundance in the shallow increased by 18% ($\beta = -0.020, p = 0.041$), and obligate corallivores declined by 11% ($\beta = 0.010, p = 0.007$), while excavators in the deeper zones declined by 18% ($\beta = 0.016, p = 0.031$), (Fig. 6). Further testing the responses of herbivore groups to changes in algal coverages (macroalgae for browsers and combined turf and DCA for grazer/detritivores, scrapers, and excavators) mirrored the earlier contrasting trajectories by depth (Online Resource 1f). Grazer/detritivore, scraper, and excavator groups increased in the shallow zones while declining in the deeper zones in response to increases in turf and DCA cover (Online Resource 1f). However, only grazer/detritivores in the shallow exhibited statistically-significant responses ($\beta = 0.001, p = 0.024$). Browsers did not show explicit responses to changes in macroalgal cover, likely due to their low abundance as well as generally low coverage of macroalgae across the sites, thus unable to build a robust model (Online Resource 1f).

At the community level, species composition after the bleaching changed significantly in deeper zones ($pseudo-F = 2.261, p = 0.005$) but not in shallow zones ($pseudo-F = 1.508, p = 0.105$) (Fig. 7). SIMPER analysis revealed that large-aggregating damselfishes (e.g. *Pomachromis richardsoni*, *Pomacentrus philippinus*, *P. moluccensis*, etc.) contributed most to community dissimilarity at both depth zones (Online Resource 2c). Shallow zones were further characterized by increases in herbivorous surgeonfishes (e.g. *Acanthurus lineatus*, *A. nigrofuscus*, and *Ctenochaetus striatus*), whereas dissimilarities in deeper zones were driven by increases in fusiliers (e.g. *Caesio caerulaurea*, *Pterocaesio digramma*). Several species exhibited significant changes in abundance. In the shallow zone, increases were detected for *Zanclus cornutus* ($p = 0.019$), *Acanthurus triostegus* ($p = 0.044$), *A. japonicus* ($p = 0.01$), *Siganus virgatus* ($p = 0.028$), and *Scarus rivulatus* ($p = 0.022$) (Online Resource 2c). In the deeper zone, significant increases were observed for *P. richardsoni* ($p = 0.007$) and *Ctenochaetus binotatus* ($p = 0.036$) (Online Resource 2c).

4. Discussion

4.1 Benthic community impacts

The 2024 mass bleaching event in Okinawa Island coincided with the highest recorded thermal stress in the region, as influenced by the El Niño phenomenon from spring of the previous year (Japan Meteorological Agency 2025a) and the reduced number of typhoons that passed through Okinawa in 2024 compared to 2023 (Japan Meteorological Agency 2025b). This led to extensive coral bleaching and subsequent mortality, particularly among *Acropora* and other coral taxa on shallow reefs. Bleaching prevalence in multiple shallow reefs surveyed (81%) were close to those reported in Sesoko Island during the 1998 event (90%; Yamazato 1999) and reported estimates from the 2016 event (50–80%) (Kayanne et al. 2017), marking this as one of the most severe episodes to date. These three events correspond to

the first, third, and fourth Global Coral Bleaching Events, underscoring the increasing frequency of heat stress events in a region once thought to have low return periods (50–60 yrs) of temperature anomalies (Thompson and van Woesik 2009). The 2024 bleaching event reduced average coral cover by more than half, accompanied by a proliferation of algal turf on recently dead corals (i.e., DCA), indicating rapid post-bleaching benthic restructuring. These impacts closely mirror those reported for the mass bleaching event on the Great Barrier Reef in 2016, where up to 50% of live coral cover was lost and algal cover increased rapidly in response to coral mortality (Stuart-Smith et al. 2018).

Coral taxon-specific responses were pronounced: shallow-water *Acropora* suffered near-total mortality, whereas *Pocillopora* and *Montipora*—typically regarded as thermally sensitive and categorized as a “loser” during the 1998 event (Loya et al. 2001; van Woesik et al. 2011)—showed notable resistance, consistent with recent findings from Afzal et al. (2025). Soft coral cover showed a slight decline, with tissue sloughing and fragmentation particularly evident in *Lobophytum*, consistent with the high susceptibility and mortality reported for soft corals during previous bleaching events (Yamazato 1999; Fabricius 1999; Loya et al. 2001). While turf algal cover on non-coral substrates remained relatively similar after bleaching, the high coral mortality presented new substrates that were rapidly colonized by turf algae, while growth of fleshy macroalgae was still negligible. These patterns suggest ongoing shifts in benthic assemblages, with future community trajectories likely shaped by the resistance and recovery capacity of individual coral taxa to recurrent bleaching events (Baker et al. 2008; Grottoli et al. 2014; Inoue and Takahashi 2014; Hughes et al. 2018).

Depth strongly mediated bleaching outcomes. Declines in coral cover and changes in community composition were more pronounced in shallow than in deeper zones. Depth-dependent variation in bleaching severity and coral mortality has been widely documented in tropical coral reefs (e.g., Bridge et al. 2014; Muir et al. 2017; Baird et al. 2018; Afzal et al. 2025) and has been largely attributed to reduced light irradiance and lower water temperatures with increasing depth, thereby mitigating thermal stress (Glynn 1996). In addition, variation in water flow and hydrodynamic regimes across depths may influence coral thermal tolerance and recovery potential (Nakamura and van Woesik 2001; Nakamura and Yamasaki 2013). Coral morphology and distribution also played roles: shallow reef flats and crests dominated by branching and corymbose corals were disproportionately affected, whereas deeper reef slopes dominated by massive and encrusting taxa tended to be more resistant (Hoegh-Guldberg and Salvat 1995; Khen et al. 2023; Kimura et al. 2025). These findings reinforce the concept that deeper reef slopes may serve as partial refugia during acute thermal stress, acting as potential sources of recruitment that may support post-disturbance recovery and resilience of coral reef ecosystems (Holstein et al. 2016; Baird et al. 2018).

Larger-scale spatial variations in terms of impacts were also evident. Declines in coral cover were markedly higher in sites along the west coast, but not in the more turbid east coast sites (Chinazaki and KGV). The eastern sites are located near a prawn aquaculture facility and river mouths, respectively, and many coral reefs along Okinawa’s east coast are characterized by higher turbidity (Hongo and Yamano 2013). While elevated turbidity and suspended sediments can negatively affect coral physiology (Bessell-

Browne et al. 2017; Jones et al. 2019; Zweifler et al. 2021), turbid environments can also reduce irradiance and buffer heat stress (Morgan et al. 2017; Browne et al. 2019; Sully and van Woesik 2020). Eastern sites were dominated by massive and encrusting corals (e.g., *Favites*, *Porites*, *Dipsastraea*, *Mycedium*, *Echinophyllia*, *Astreopora*) which are known to have thicker tissues and generally tend to be more thermally tolerant than fast-growing branching corals (e.g. *Acropora*) (Loya et al. 2001; Pratchett et al. 2013; Yeung et al. 2025). Furthermore, persistent bleached colonies were observed at Chinazaki three months after the event (Online Resource 1g), suggesting limited recovery or potential heterotrophic survival strategies in these turbid environments (Anthony and Fabricius 2000; Bessell-Browne et al. 2014; Kishimoto et al. 2020). These site-specific assemblage differences likely underpin the spatial heterogeneity of bleaching severity and resultant communities across Okinawan reefs.

4.2 Fish responses

Near-term responses of reef fishes to the 2024 bleaching were generally weak and limited to specific functional groups. Species richness and Shannon diversity showed little change across sites and depth zones, suggesting that drastic changes such as species losses through extirpation or emigration are less likely to occur immediately after bleaching (< 6 months, as in this study) (Wilson et al. 2006; Pratchett et al. 2008, 2011). Although declines in species richness (e.g., Sano 2004) and diversity (e.g., Shibuno et al. 1999) have been documented shortly after bleaching, most of these changes were limited to coral specialists. Stronger declines may emerge over longer terms in the absence of substantial recovery, consistent with reports that fish communities often exhibit lagged responses to coral mortality (Graham et al. 2007; Pratchett et al. 2011), especially when structural complexity remains intact (Sano 2004; Wilson et al. 2006; Pratchett et al. 2008; Graham et al. 2009, 2015). Interestingly, species richness and Shannon diversity increased in Kakinouchi—the site with the most severe bleaching outcomes—likely due to community shuffling. Extensive coral mortality may increase resource heterogeneity and prompt temporary range expansions and altering foraging behavior in response to shifts in algal or coral prey availability (Garpe et al. 2006; Wilson et al. 2006; Pratchett et al. 2011; Wismer et al. 2019). Given this, many previously unrecorded taxa from adjacent habitats (e.g., rubble-associated species) in this site were more frequently observed in formerly coral-dominated areas. These movements may be further facilitated by the breakdown of coral territories maintained by many dominant corallivores including butterflyfishes and damselfishes (Ceccarelli and Jones 2001; Samways 2005; Keith et al. 2018).

Responses to coral loss varied among functional groups and were further influenced by depth zones. Only obligate corallivores showed a clear coral-limited signal, mirroring sharp declines in shallow zones where coral mortality was more severe, whereas populations in deeper zones were more buffered from effects of extensive coral loss (Gomez et al. 2025b). This outcome aligns with the tight dietary dependence of obligate corallivores on corals (Pratchett 2005; Gomez et al. 2025b) and echoes findings for other highly coral-dependent species such as coral gobies and some damselfishes after disturbances (Booth and Beretta 2002; Sano 2004; Coker et al. 2012; Pratchett et al. 2012). Herbivorous groups (grazers/detritivores, scrapers and excavators) responded to coral loss indirectly. These groups increased in shallow zones, presumably tracking the proliferation of turf on recently dead coral skeletons

(Garpe et al. 2006; Wilson et al. 2006; Pratchett et al. 2008), as further suggested by their coupled declines in deeper zones. The trend persisted when these groups were tested against percent change in turf and DCA, since these algal variables were directly correlated with coral mortality. While general herbivore increase is typical of post bleaching scenarios (e.g., Shibuno et al. 1999; McClanahan et al. 2002; Garpe 2006), and in contrast to the increase in browsing herbivores and fleshy macroalgae in GBR after the 2016 bleaching (Stuart-Smith et al. 2018), we did not observe a clear pattern for browsers, given that both browser abundance and macroalgae cover were generally low across sites. Nonetheless, browser responses may be expected over time as macroalgal shifts may come at much later stages (Diaz-Pulido and McCook 2002) and may also be highly influenced by other factors such as seasonality, nutrient levels, and herbivory rates (McClanahan et al. 2001). Other functional groups exhibited only minor declines or flat trends in response to coral loss, reflecting broader dietary flexibility as generalists (Wilson et al. 2006) or weaker associations with live coral (Muruga et al. 2024). It should be noted however that while these broad functional groups offer a coarse lens of responses for different fish types, some responses may be more severe for specific taxa as governed by their ecological specializations (Munday 2004; Wilson et al. 2006).

Community-level analyses further reinforce these benthos-fish linkages while highlighting the complexity of interpreting short-term responses. Shallow assemblages remained compositionally stable despite pronounced coral mortality, whereas deep assemblages shifted significantly. This disparity may reflect spatial redistribution, with fishes shuffling between depths or reef zones rather than being lost entirely (Garpe et al. 2006; Wismer et al. 2019). Many of the species contributing most to dissimilarity (e.g., large aggregating damselfishes, fusiliers, roving surgeonfishes and parrotfishes) are highly mobile and stochastic in their occurrence, making it difficult to fully disentangle bottom-up effects from transient or seasonal fluctuations (Pratchett et al. 2011). Sustained monitoring will therefore be essential in clarifying these longer-term trajectories in relation to benthic and environmental shifts.

5. Conclusion

The 2024 mass bleaching event in Okinawa Island was a significant event in the long history of disturbances in this region. Bleaching prevalence was high and mortality was extensive, particularly in the shallow reefs dominated by *Acropora*. In contrast, other genera previously considered as “losers” during bleaching such as *Pocillopora* and *Montipora*, showed high resistance. These depth- and taxon-specific responses drove significant shifts in benthic communities, underscoring the uneven impacts of thermal stress across habitats and coral assemblages. Immediate changes in fish diversity and functional group abundance in response to coral loss were generally weak and restricted to obligate corallivores. Short-term fish responses were further modulated by depth, reflecting potential compensatory dynamics linked to resource availability or transient movement rather than demographic loss. Together, these findings provide an important ecological baseline for Okinawan reefs in the wake of an unprecedented bleaching event. While some corals and fishes demonstrated resistance in the near term, the persistence of these patterns under ongoing warming remains uncertain. Continued long-term

monitoring will remain essential in determining whether near-term stability persists or masks delayed ecological shifts that could undermine biodiversity and reef functioning.

Declarations

Competing interests

The authors declare no competing interests.

Funding

This study was supported in part by the Japan Science Society Sasakawa Foundation Grant (2024–4017) to L.Y.K., the Suzuki Shohei Marine Biological Research Grant from the University of the Ryukyus to R.G., and the Japan Society for the Promotion of Science (JSPS) KAKENHI (Grant 23H03560) to T.N. R.G. was supported by a scholarship from the Japan Ministry of Education, Culture, Sports, Science and Technology (MEXT).

Author Contribution

Conceptualization: Lucas Yutaka Kimura, Rickdane Gomez **; Methodology:** Lucas Yutaka Kimura, Rickdane Gomez **; Data Curation:** Lucas Yutaka Kimura, Rickdane Gomez **; Formal analysis and investigation:** Lucas Yutaka Kimura, Rickdane Gomez **; Writing – original draft preparation:** Lucas Yutaka Kimura, Rickdane Gomez **; Writing – review and editing:** Lucas Yutaka Kimura, Rickdane Gomez, Takashi Nakamura **; Funding acquisition:** Lucas Yutaka Kimura, Rickdane Gomez, Takashi Nakamura **; Resources:** Lucas Yutaka Kimura, Rickdane Gomez, Takashi Nakamura **; Supervision:** Takashi Nakamura.

Acknowledgement

We are grateful to Faezeh Zare, Yuta Higa, and Ibuki Higa for their assistance during field surveys, and to Jue Lalas for aid in soft coral identification.

Data Availability

Data is available upon request.

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Figures

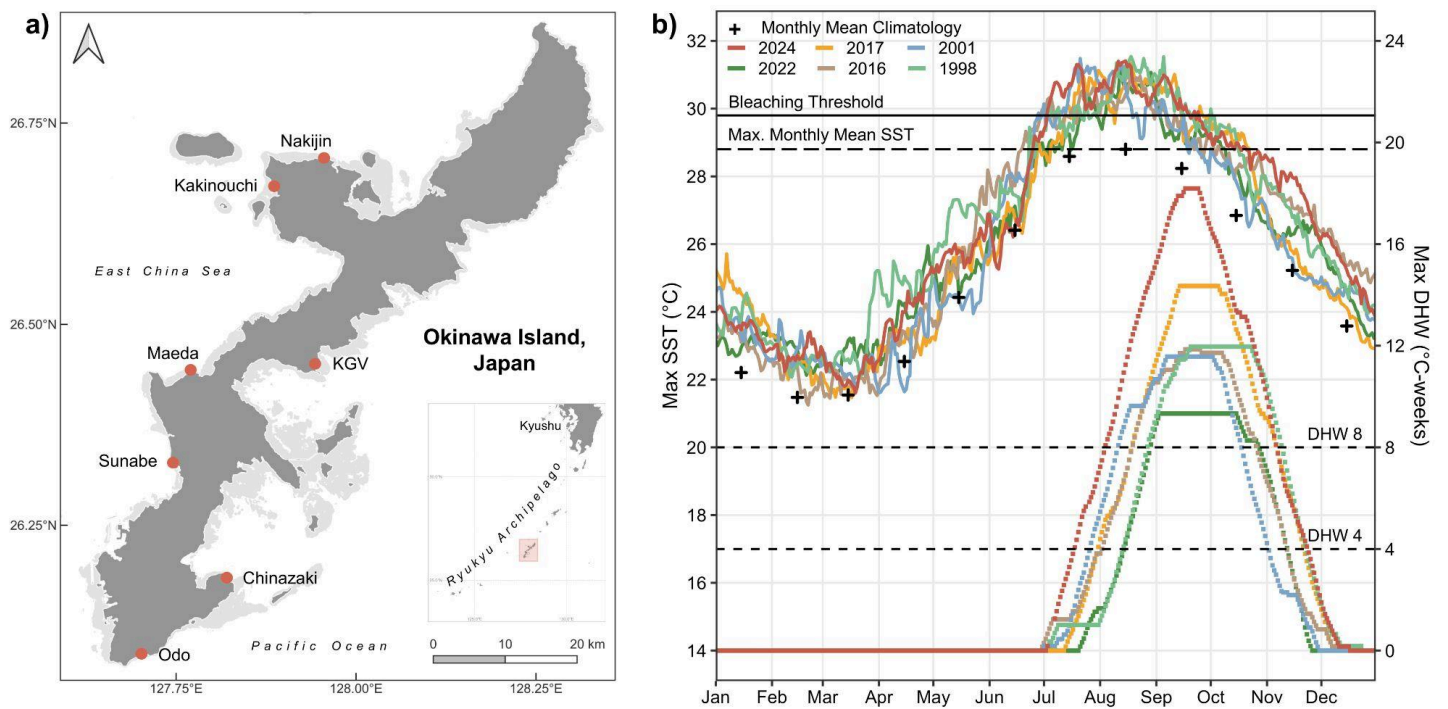


Figure 1

Map of study locations, with gray shading representing shallow reef extent (a) and line graph of temperature trends during the most recent and previous major (DHW > 8) bleaching years in Okinawa Island, Japan (b). Sea Surface Temperature (SST) and Degree Heating Week (DHW) values were obtained from NOAA Coral Reef Watch 5 km resolution as the maximum daily value across grid cells for Okinawa Island

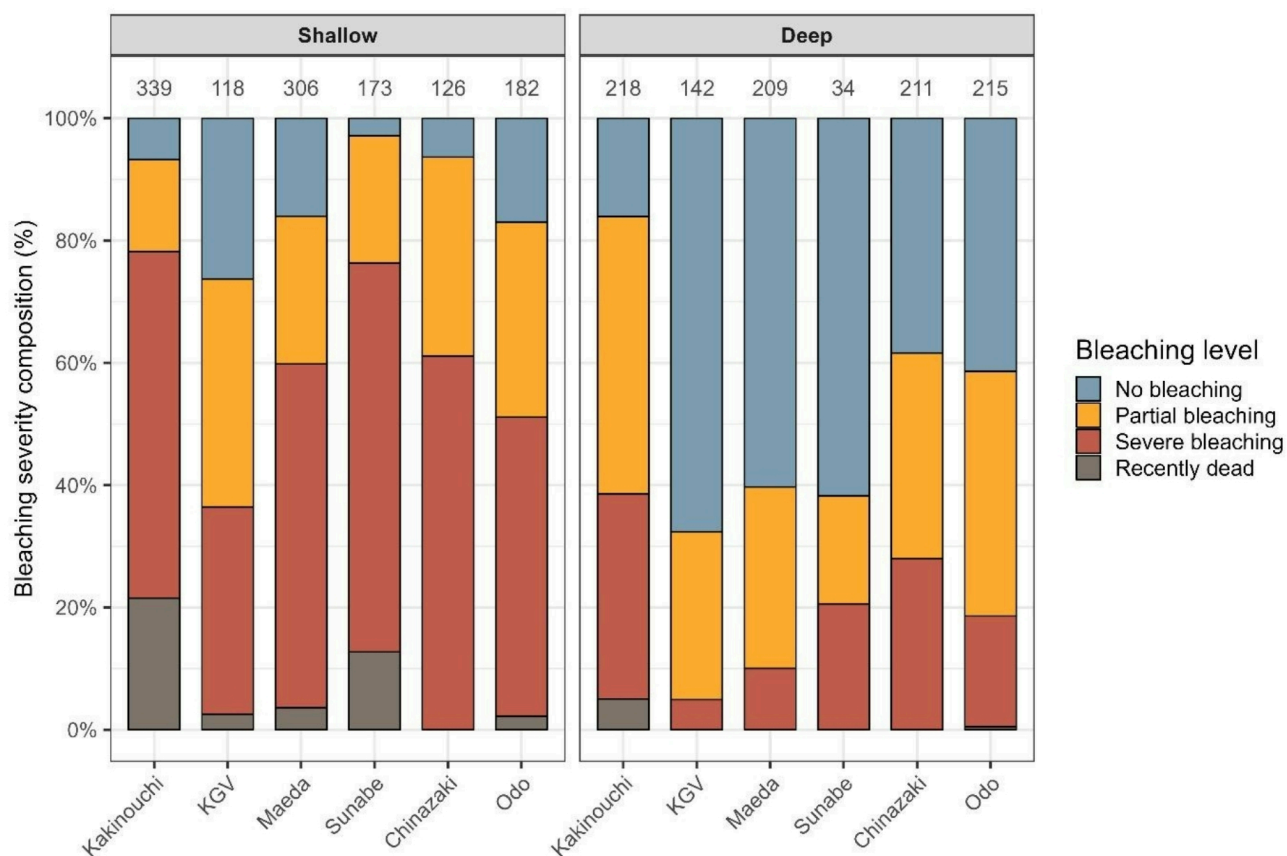


Figure 2

Bleaching severity composition of hard corals across sites per depth zone. Numbers above bars indicate the total number of hard coral points assessed from photos at each location. Surveys were conducted in August 2024. Site Nakijin was not assessed during this period

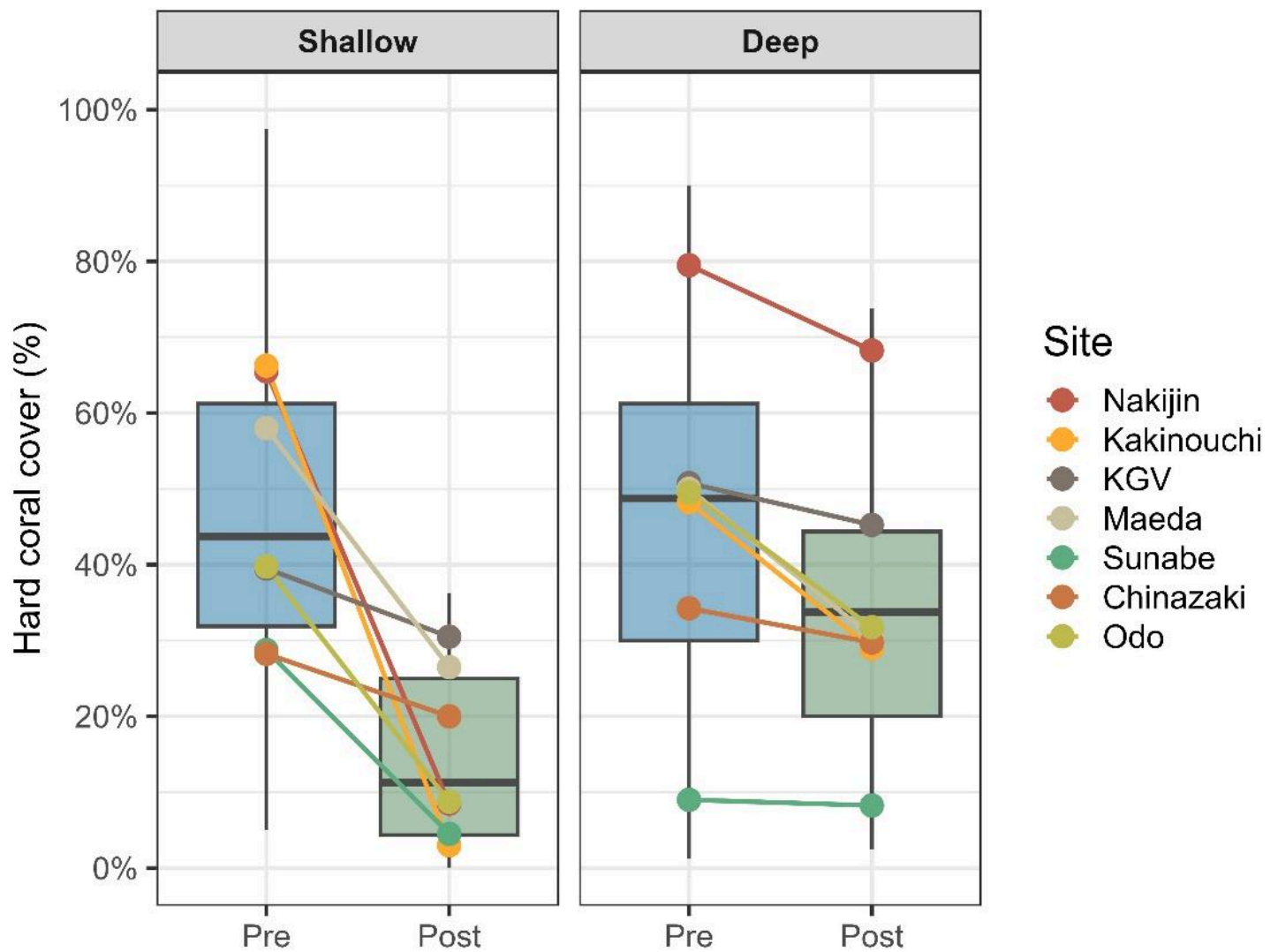


Figure 3

Changes in hard coral cover before and after bleaching for each depth zone. Boxes represent interquartile ranges, horizontal lines represent the median across replicates, and connected points represent site-level means

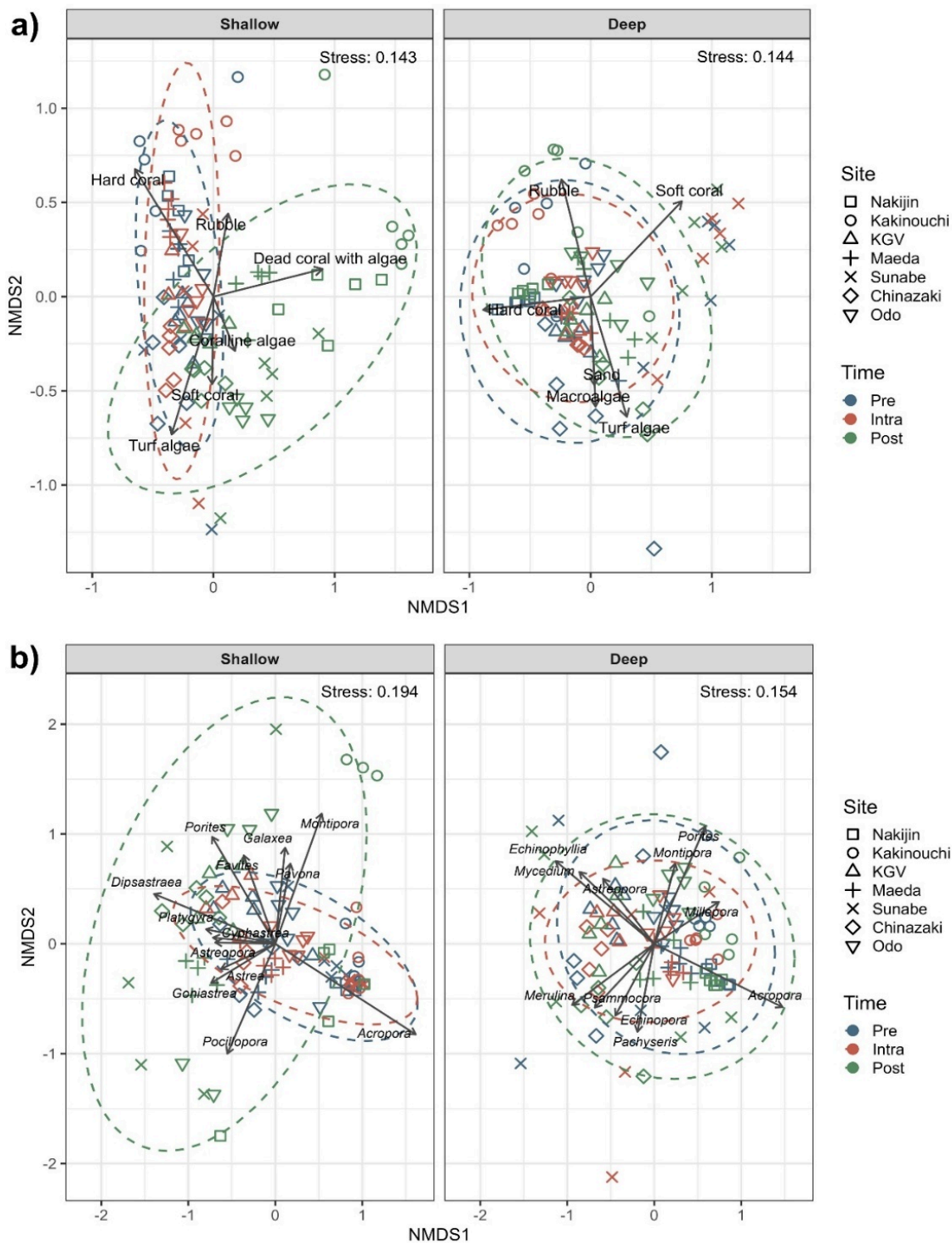


Figure 4

NMDS ordinations of benthic communities (a) and coral composition (b) on untransformed Bray-Curtis matrices. Points represent individual transects. Arrow vectors indicate substrates significantly driving community differences ($p < 0.05$) determined through *envfit* function in the *vegan* package (Oksanen et al. 2022), while ellipses indicate 95% confidence intervals

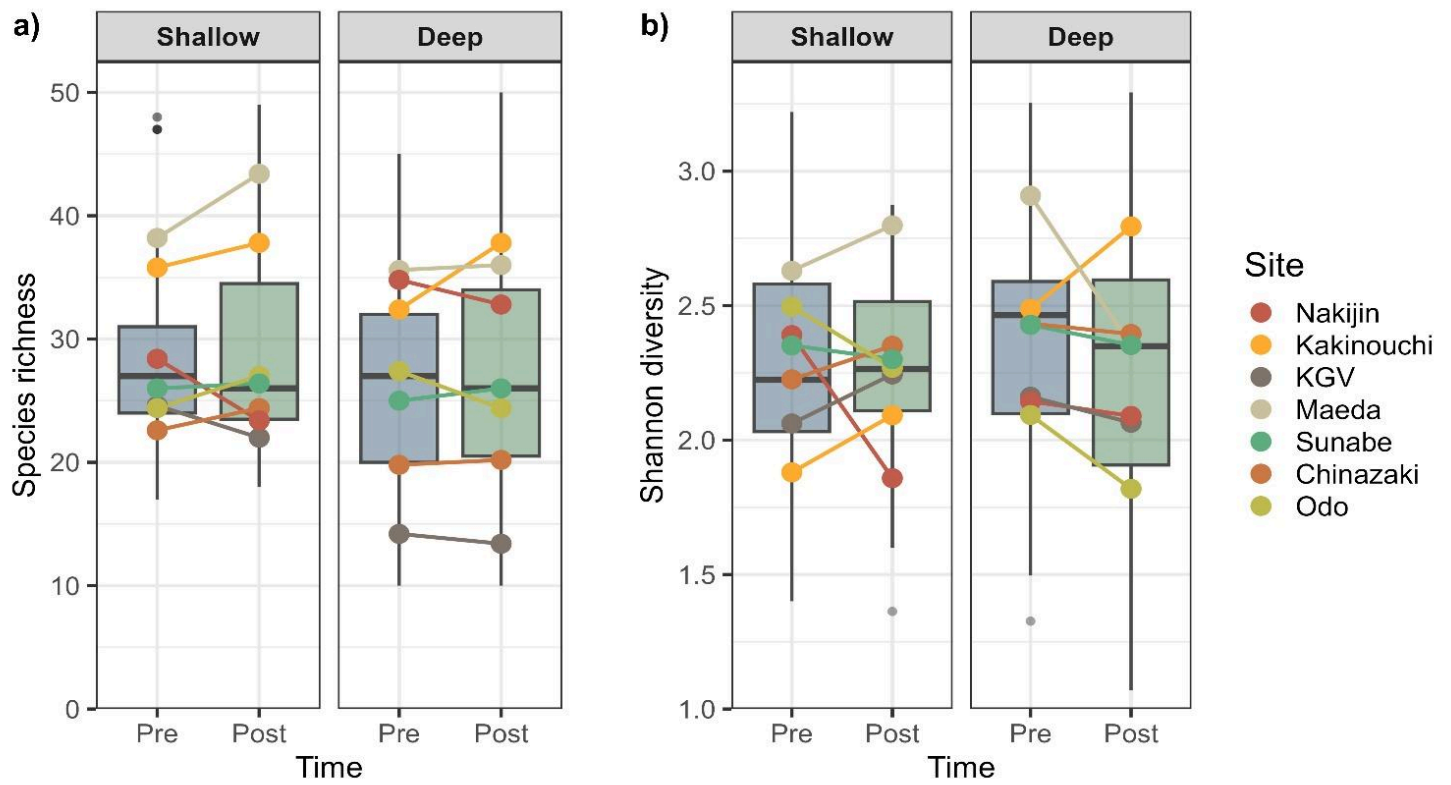


Figure 5

Changes in mean (a) species richness and (b) Shannon diversity before and after bleaching. Boxes represent interquartile ranges, horizontal lines represent the median value across replicates, and points represent site-level means

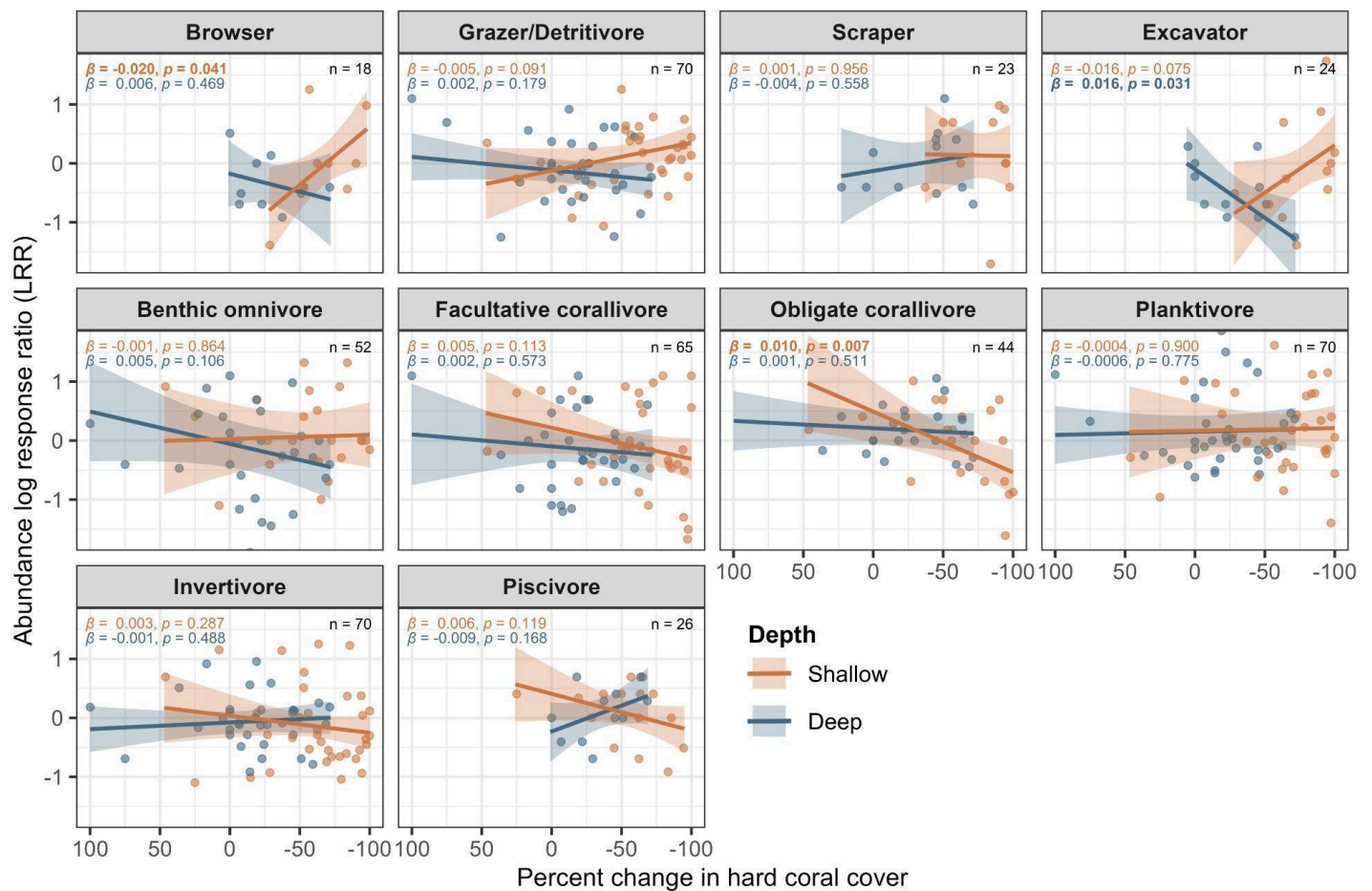


Figure 6

GLMM trends showing the responses of fish functional groups (abundance log response ratio) to percent changes in hard coral cover. The x-axis is reversed to visualize coral loss post-bleaching. n represents the number of transects where individuals belonging to specified functional groups were recorded. Model coefficients (β) and p-values in bold indicate statistically significant changes

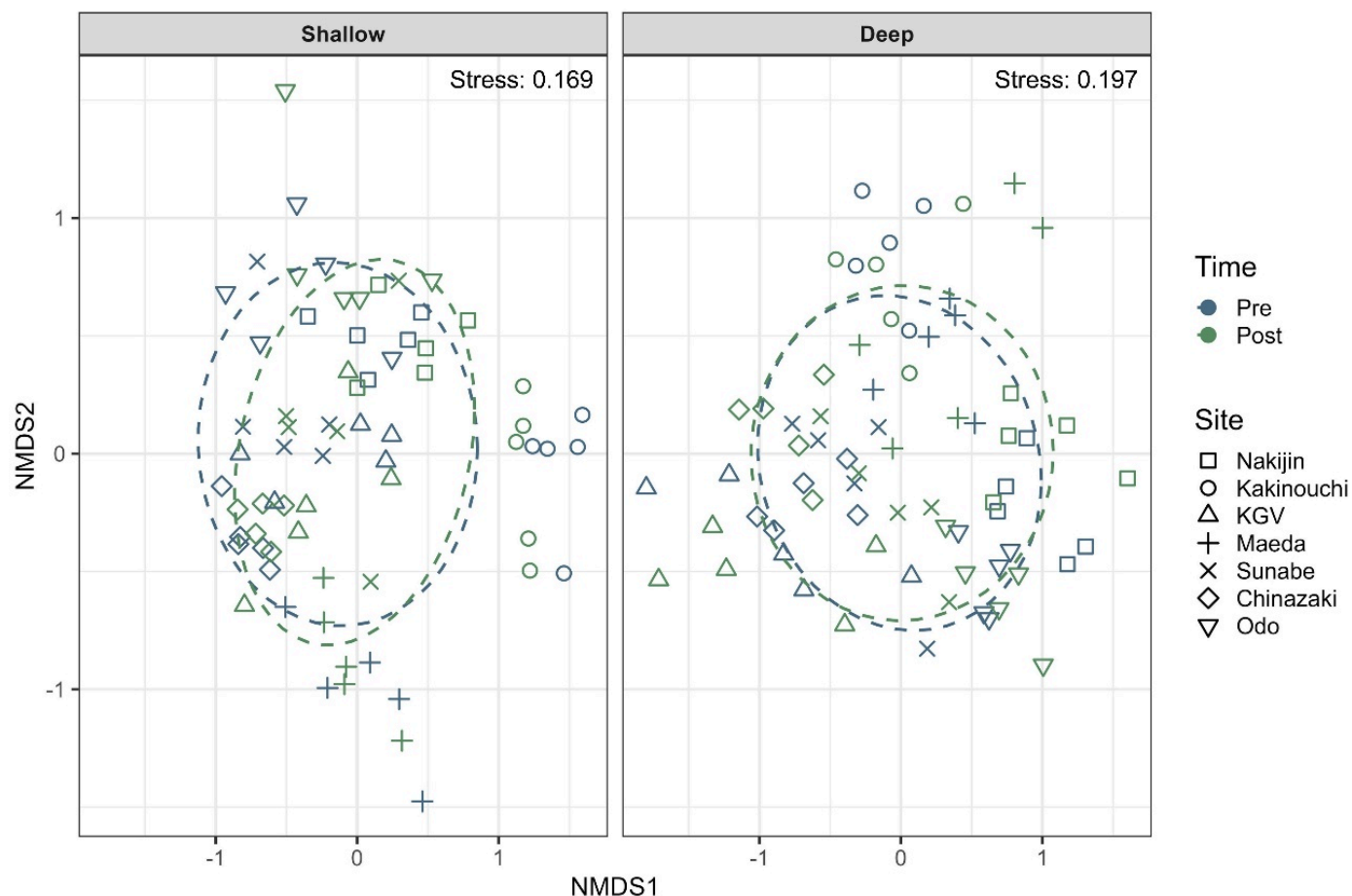


Figure 7

Non-metric multidimensional scaling (NMDS) ordination of fish communities on Hellinger-transformed Bray-Curtis matrix. Points represent individual transects while ellipses indicate 95% confidence intervals

Supplementary Files

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