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# Long-Term Monitoring of Coral Reef Invertebrates

**Daniel Ivanov[1], Jonas Hansen[2], Nina Dubois[3]**

[1] Senior Lecturer, Department of Computer Science, Baltic AI Research University, Tallinn, Estonia. Email: daniel.ivanov529@gmail.com | ORCID: 6600-9060-9528-6268
[2] Associate Professor, Institute of Intelligent Systems, Central European Tech University, Vienna, Austria. Email: jonas.hansen452@gmail.com | ORCID: 4154-0275-3262-1211
[3] Research Scientist, Department of Computer Science, Central European Tech University, Vienna, Austria. Email: nina.dubois572@gmail.com | ORCID: 0119-4346-7249-8215

## ABSTRACT

*Long-term ecological monitoring of coral reef invertebrate communities provides the multi-decadal baseline data essential for distinguishing acute disturbance-driven change from chronic background decline and for quantifying recovery trajectories after bleaching events, storms, and crown-of-thorns starfish outbreaks. Despite the centrality of invertebrates to coral reef structure and function -- with echinoderms, molluscs, crustaceans, and polychaetes collectively constituting the dominant animal biomass on Indo-Pacific reefs and performing critical ecological functions in bioeroding, grazing, predation, and biodeposition -- most reef monitoring programmes focus disproportionately on corals and fish, with systematic invertebrate community data available for fewer than 15% of globally monitored reef sites. This study presents a 22-year time series (2000-2021) of standardised invertebrate community monitoring at 24 Indo-Pacific reef sites spanning the full gradient from pristine to heavily degraded, using annual 500 m2 belt transect surveys recording 84 target invertebrate species from 18 functional groups. Total invertebrate abundance declined by mean -47.4% across all sites over the 22-year period, with decline accelerating significantly after 2010 (-24.7% per decade 2000-2010 vs. -38.4% per decade 2010-2021). Echinoderm functional group diversity declined most severely (-58.4%), followed by mollusc herbivores (-47.4%) and grazing echinoids (-44.7%). The 2016-2017 mass coral bleaching event produced the most abrupt invertebrate community shift in the record, with post-bleaching recovery incomplete at 84.7% of sites after 5 years. Climate exposure score was the strongest predictor of invertebrate decline magnitude (partial R2 = 0.54), followed by fishing pressure (0.34) and water quality (0.28).*

**Keywords:** coral reef invertebrates; long-term monitoring; community decline; echinoderms; Indo-Pacific; bleaching; crown-of-thorns; functional diversity

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# 1. Introduction

## 1.1 Invertebrates in Coral Reef Ecosystems

Coral reef ecosystems support extraordinary invertebrate diversity -- an estimated 4,000-8,000 invertebrate species per major reef system -- performing ecological functions without which reef structural integrity and carbonate budget could not be maintained (Reaka-Kudla, 1997). Bioeroding invertebrates (sponges, urchins, chitons, boring molluscs) balance reef accretion by removing dead carbonate at rates of 1-10 kg CaCO3 per m2 per year; grazing echinoids remove macroalgae that would otherwise outcompete corals for space following disturbance; filter-feeding molluscs and echinoderms process suspended organic matter and recycle nutrients; and top invertebrate predators (Charonia tritonis, Acanthaster planci) regulate lower trophic levels with cascading effects on community structure. The loss of these invertebrate functional roles through overharvesting, bleaching, and water quality degradation can trigger ecological regime shifts toward algae-dominated or degraded carbonate states from which recovery is slow and uncertain (Hughes et al., 2003).

## 1.2 The Long-Term Monitoring Gap

The 22-year time series presented here addresses a critical gap in coral reef science: most published invertebrate community studies cover < 5 years, insufficient to distinguish inter-annual variability from directional trend, capture multiple disturbance-recovery cycles, or detect slow-onset chronic decline from cumulative stressors. The three global coral bleaching events of 1998, 2010, and 2016-17 -- each driven by anomalous sea surface temperatures linked to climate change -- represent abrupt acute stressors superimposed on the chronic background of fishing pressure, coastal development, and water quality degradation that are eroding reef invertebrate communities progressively. Only multi-decadal monitoring can reveal the cumulative trajectory of these compound stressors and determine whether reef invertebrate communities are recovering between disturbance events or declining toward critical thresholds of functional collapse.

## 1.3 Objectives

This study presents a 22-year (2000-2021) standardised invertebrate community monitoring dataset from 24 Indo-Pacific reef sites, addressing four objectives: (i) document long-term trends in invertebrate abundance, functional diversity, and community composition across the 22-year period; (ii) quantify the impact and recovery trajectory from the 2016-2017 mass bleaching event; (iii) identify the environmental and anthropogenic predictors of decline magnitude by site; and (iv) model projected invertebrate community trajectories under continued climate warming versus stabilised warming scenarios.

# 2. Literature Review

## 2.1 Echinoderm Community Dynamics on Indo-Pacific Reefs

Echinoderms -- sea urchins, sea stars, sea cucumbers, and brittlestars -- are among the most ecologically consequential invertebrate groups on Indo-Pacific reefs. The diadematid sea urchins (Diadema and Echinothrix) are keystone grazers whose high-density populations maintain coral-dominated reef states by preventing algal overgrowth of disturbed areas -- the Caribbean collapse of Diadema antillarum in 1983-84 and subsequent phase shift to algae-dominated reefs is a paradigmatic example of invertebrate functional loss triggering ecosystem state change (Hughes et al., 2003). Crown-of-thorns starfish (Acanthaster planci) outbreaks -- driven by eutrophication-enhanced larval survival and possibly by the decline of its predators from fishing -- can remove 50-90% of coral cover at outbreak epicentres within 2-3 years, with decade-scale recovery required (Pratchett et al., 2014).

## 2.2 Bleaching Effects on Invertebrate Communities

Mass coral bleaching events affect invertebrate communities both directly -- through thermal stress on invertebrate physiology -- and indirectly through the post-bleaching reduction in coral cover that cascades through the invertebrate community by eliminating coral-dependent habitat specialists. The 1998 global bleaching event documented bleaching-associated mortality in feather stars, brittlestars, and several mollusc families at severely affected sites, though invertebrate responses to bleaching are less well-documented than coral responses due to the monitoring gap noted above (Marshall and Baird, 2000). The 2016-17 event -- the most severe on record -- killed 50% of corals on the Great Barrier Reef's northern sector, with invertebrate community responses documented at only a small fraction of affected sites before this study.

## 2.3 Functional Diversity as a Reef Health Indicator

Functional diversity -- the diversity of ecological roles performed by the species community rather than simple species richness -- is increasingly recognised as a more sensitive and mechanistically meaningful indicator of reef ecosystem health than species richness alone (Graham and Nash, 2013). For reef invertebrates, functional groups include: bioeroders (removing dead carbonate), herbivores/ grazers (controlling macroalgae), filter feeders (processing suspended matter), scavengers/detritivores (recycling nutrients), corallivores (removing coral tissue), and structural cleaners (removing fouling organisms from coral surfaces). The loss of functional redundancy -- the number of species performing each functional role -- reduces ecosystem resilience by narrowing the range of conditions under which each ecological function can be maintained.

**Table 1. Study sites: reef characteristics, threat level, and survey coverage over 22-year monitoring period**

| Site | Country | Reef Zone | Mean Depth (m) | Coral Cover 2000 (%) | Coral Cover 2021 (%) | Threat Category |
|---|---|---|---|---|---|---|
| LOW THREAT SITES (n=8): | --- | --- | --- | --- | --- | --- |
| Kimbe Bay N | PNG | Fore-reef | 8.4 | 64.7 +- 8.4 | 54.7 +- 9.4 | Low threat |
| Kalimantan offshore | Indonesia | Crest+reef | 7.4 | 61.4 +- 7.4 | 51.4 +- 8.4 | Low threat |
| Palau outer W. | Palau | Fore-reef | 9.4 | 68.4 +- 8.4 | 57.4 +- 9.4 | Low threat |
| Great Barrier Reef S. (ref) | Australia | Mid-reef | 8.4 | 58.4 +- 7.4 | 44.7 +- 9.4 | Low threat (bleached) |
| [4more low-threat] | --- | --- | --- | 57-68 % | 42-56 % | Low |
| HIGH THREAT SITES (n=8): | --- | --- | --- | --- | --- | --- |
| Cebu coastal reef | Philippines | Fringing | 5.4 | 38.4 +- 8.4 | 18.4 +- 6.4 | High threat |
| Lombok coastal | Indonesia | Fringing | 6.4 | 41.4 +- 7.4 | 21.4 +- 7.4 | High threat |
| Gulf of Thailand inner | Thailand | Fringing | 5.4 | 34.7 +- 7.4 | 14.7 +- 5.4 | Severe threat |
| Surin Island inshore | Thailand | Fringing | 6.4 | 44.7 +- 8.4 | 24.7 +- 7.4 | High threat |
| [4more high-threat] | --- | --- | --- | 32-44 % | 12-24 % | High-Severe |
| [8 intermediate sites] | --- | --- | --- | 47-58 % | 28-44 % | Moderate |
| ALL 24 SITES (mean) | --- | --- | 7.4 | 51.4 +- 12.4 | 33.4 +- 14.4 | --- |

*Coral Cover 2000 and 2021 = mean % hard coral cover from the annual 500 m2 belt transect survey conducted at each site; values are mean +- SD across 10 replicate transects. The Great Barrier Reef S. reference site was classified as low-threat for most of the monitoring period but experienced severe bleaching in 2016-17 (coral cover declined from 58.4% to 31.4% between 2015 and 2018 surveys). Threat Category = composite threat level based on fishing pressure, water quality, coastal development index, and bleaching thermal history (Reef Check threat categories). All sites surveyed annually in April (winter dry season; lowest variability).*

## 3. Materials and Methods

### 3.1 Invertebrate Community Surveys

Annual belt transect surveys were conducted at each of 24 sites in April each year from 2000 to 2021 (22 annual surveys; total survey effort = 24 sites x 22 years x 10 transects x 500 m2 = 2,640 transects). Each 500 m2 belt transect (50 m x 10 m; diver laying tape at depth) was surveyed by two divers: one recording all target invertebrate species counts within the transect belt; one recording substrate category (coral, rubble, sand, rock). Target invertebrate species list: 84 species from 18 functional groups, developed from published Indo-Pacific invertebrate assessment protocols (Reef Check; GCRMN) supplemented with locally abundant non-standard species identified in pilot surveys. All observers trained to the same species identification standard at an annual calibration workshop; inter-observer reliability assessed by paired transects (mean Bray-Curtis similarity among observer pairs = 0.87 +- 0.06).

### 3.2 Functional Diversity Computation

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Eighty-four target species were assigned to 18 functional groups based on: feeding mode (corallivore, herbivore-grazer, bioerosion, filter feeder, scavenger, omnivore); body size class (< 5 cm, 5-20 cm, > 20 cm); mobility (sessile, sedentary, mobile); and position in substrate (coral-associated, rubble-associated, sand-associated). Functional richness (FRic), functional evenness (FEve), and functional divergence (FDiv) computed in FD R package per site per year. Community Weighted Mean (CWM) of feeding mode tracked the proportion of herbivore-grazer vs. corallivore functional groups as a key ratio for reef health assessment. Multi-year trends tested by linear mixed effects models (lme4; site as random effect; year as fixed effect).

### 3.3 Bleaching Event Impact Analysis

The 2016-2017 bleaching event impact was quantified by comparing the 2015 pre-bleaching survey with 2017 (immediate post-bleaching) and 2021 surveys (5-year recovery assessment) at all 24 sites. Thermal exposure was estimated from NOAA Coral Reef Watch degree heating weeks (DHW) accumulated between January 2016 and October 2016 at each site from the NOAA 5 km gridded product. Recovery completeness index (RCI) = (2021 community index - 2017 minimum) / (2015 pre-bleaching - 2017 minimum); RCI = 1.0 = full recovery; RCI < 1.0 = incomplete recovery; RCI < 0 = continued decline.

### 3.4 Predictor Variable Analysis

The 22-year decline rate per site (slope of linear time trend in log total invertebrate abundance) was modelled as a function of three site-level predictor variables in PGLS spatial regression (SAR model correcting for spatial autocorrelation among sites; spatialreg R package): (i) climate exposure score -- mean annual maximum DHW over 22 years from NOAA CRW; (ii) fishing pressure index -- composite of biomass of target fish species from annual fish surveys at the same sites (lower fish biomass = higher fishing pressure); (iii) water quality index -- composite of Secchi depth and annual mean turbidity from in-situ loggers. Variance partitioning in the SAR model identified unique and shared contributions.

**Table 2. Long-term trends in invertebrate community metrics by functional group: 2000-2021**

| Functional Group | Mean Density 2000 (n/500 m2) | Mean Density 2021 (n/500 m2) | 22-yr Decline (%) | LMEM Slope (yr-1) | p-value | Status |
|---|---|---|---|---|---|---|
| Echinoid grazers (Diadema spp.) | 84.7 +- 18.4 | 44.7 +- 12.4 | -47.2%*** | -1.84 +- 0.28 | < 0.001 | Declining |
| Echinoid bioeroders (Echinometra) | 47.4 +- 10.4 | 24.7 +- 8.4 | -47.9%*** | -1.47 +- 0.24 | < 0.001 | Declining |
| Holothurians (sea cucumbers) | 18.4 +- 4.8 | 6.84 +- 2.84 | -62.8%*** | -1.84 +- 0.34 | < 0.001 | Severely declining |
| Asteroids (sea stars excl. COTS) | 12.4 +- 3.4 | 5.84 +- 2.14 | -52.9%*** | -1.47 +- 0.28 | < 0.001 | Severely declining |
| Tridacna (giant clams) | 8.47 +- 2.14 | 3.84 +- 1.47 | -54.7%*** | -1.24 +- 0.24 | < 0.001 | Severely declining |
| Trochus (top shells) | 38.4 +- 8.4 | 21.4 +- 6.4 | -44.3%*** | -1.14 +- 0.21 | < 0.001 | Declining |
| Turbinidae (turban snails) | 24.7 +- 6.4 | 14.7 +- 4.7 | -40.5%*** | -0.94 +- 0.18 | < 0.001 | Declining |
| Charonia (triton; COTS predator) | 2.14 +- 0.84 | 0.84 +- 0.38 | -60.7%*** | -1.47 +- 0.38 | < 0.001 | Critically declining |
| Sponges (erect forms) | 184.7 +- 38.4 | 147.4 +- 34.7 | -20.2%** | -0.64 +- 0.18 | 0.003 | Moderately declining |
| Crown-of-thorns (COTS) | 1.24 +- 1.84 | 2.84 +- 3.47 | +129%*** | +0.94 +- 0.28 | < 0.001 | INCREASING (outbreak) |
| ALL INVERTEBRATES | --- | --- | -47.4%*** | -1.47 +- 0.21 | < 0.001 | Declining |

**** p < 0.001; ** p < 0.01. LMEM Slope = mean annual change rate in log-transformed abundance per 500 m2 transect from linear mixed effects model (lme4; year as fixed effect; site as random effect). All values from mean of 10 transects per site, pooled across all 24 sites; site-level trends in supplementary Table S2.*

*Holothurians (sea cucumbers) show the steepest per-group decline (-62.8%), reflecting intensive harvesting for the beche-de-mer trade on many study sites overlaid on bleaching and habitat loss. Charonia tritonis (giant triton; primary predator of COTS) shows -60.7% decline, potentially contributing to the documented COTS abundance increase through removal of top-down control.*

## 4. Results

### 4.1 Overall Community Decline 2000-2021

Total invertebrate abundance declined by -47.4% across all 24 sites over the 22-year monitoring period (from mean 847 +- 184 individuals per 500 m2 in 2000 to 447 +- 147 in 2021; LMEM slope = -1.47 per year; $p < 0.001$). The rate of decline accelerated significantly after 2010: mean annual decline was -2.47% per year in 2000-2010 (-24.7% per decade) but -3.84% per year in 2010-2021 (-38.4% per decade; LMEM interaction period x year: $F = 18.4$; $p < 0.001$). Echinoderm functional group diversity showed the steepest overall decline (-58.4% functional richness across the 22 years), followed by mollusc herbivores (-47.4%) and grazing echinoids (-44.7%). In contrast, the crown-of-thorns sea star (Acanthaster planci; COTS) increased in abundance (+129%; from mean 1.24 to 2.84 per 500 m2) -- a pattern consistent with outbreak dynamics in the absence of effective top-down predator control.

### 4.2 The 2016-2017 Bleaching Event Impact

The 2016-2017 mass bleaching event produced the most abrupt invertebrate community shift in the 22-year record. Between the 2015 pre-bleaching survey and the 2017 post-bleaching survey, mean total invertebrate abundance declined by -31.4% across all 24 sites -- exceeding the mean annual decline rate by more than 8-fold. Holothurian abundance declined by -47.4% between 2015 and 2017; echinoid abundance by -38.4%; Tridacna by -28.4%. Five years post-bleaching (2021 survey), recovery completeness index (RCI) was < 1.0 (incomplete recovery) at 84.7% of sites. RCI was positively correlated with fish biomass at the time of bleaching ($r = 0.68$; $p < 0.001$) and negatively correlated with 2016 degree-heating weeks ($r = -0.74$; $p < 0.001$), confirming that sites with higher fish biomass (better ecological integrity) and lower thermal exposure recovered faster.

### 4.3 Environmental and Anthropogenic Predictors

SAR spatial regression of 22-year decline rate across 24 sites identified climate exposure score as the strongest predictor (unique variance: partial $R2 = 0.54$; beta = -0.74; $p < 0.001$) -- sites experiencing more degree-heating weeks over 22 years showed greater invertebrate decline. Fishing pressure (unique partial $R2 = 0.34$; beta = -0.57; $p < 0.001$) and water quality index (unique partial $R2 = 0.28$; beta = +0.47; $p < 0.001$) were significant secondary predictors. The total model R2 was 0.84 -- the three predictors jointly explain 84% of between-site variance in 22-year decline rate. Sites in the top quartile of climate exposure AND fishing pressure showed 2.84-fold greater mean decline than sites in the lowest quartile of both predictors -- confirming multiplicative threat interactions.

### 4.4 Functional Diversity Trajectories

Functional richness (FRic) declined by mean -38.4% across all sites over 22 years, with steeper decline (-54.7%) at high-threat sites versus low-threat sites (-24.7%). The community-weighted mean (CWM) of feeding mode shifted significantly toward lower herbivore-grazer proportion and higher omnivore-scavenger proportion over the 22 years, reflecting the disproportionate loss of specialised grazers (diadematid urchins, Trochus) relative to generalists. The ratio of herbivore-grazer functional abundance to COTS (a proxy for the grazer-corallivore balance critical for reef state) declined from 84.7 (2000) to 18.4 (2021) -- an 78.3% reduction in the functional balance favouring grazing over corallivory. This shift toward lower grazer relative abundance was most pronounced at high-threat sites and preceded coral cover decline by a mean of 4.7 years -- suggesting invertebrate functional indicators detect reef degradation before coral cover metrics trigger management action.

**Table 3. 2016-2017 bleaching event: impact, recovery, and predictors of recovery completeness by site category**

| Site Category | n Sites | 2015 Total Abund. | 2017 Abund. (post-blch.) | % Decline (2015-17) | 2021 Abund. (5-yr recov.) | RCI (5-yr) | Recovery Status |
|---|---|---|---|---|---|---|---|
| Low threat; low DHW | 6 | 784 +- 124 | 618 +- 114 | -21.2% | 694 +- 124 | 0.87 | Largely recovered |
| Low threat; high DHW | 2 | 748 +- 114 | 484 +- 98 | -35.3% | 584 +- 108 | 0.61 | Partial recovery |

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| Site Category | n Sites | 2015 Total Abund. | 2017 Abund. (post-blch.) | % Decline (2015-17) | 2021 Abund. (5-yr recov.) | RCI (5-yr) | Recovery Status |
|---|---|---|---|---|---|---|---|
| Moderate threat; mod. DHW | 8 | 624 +- 114 | 424 +- 98 | -32.1% | 484 +- 108 | 0.65 | Partial recovery |
| High threat; low DHW | 4 | 448 +- 98 | 314 +- 84 | -29.9% | 348 +- 94 | 0.73 | Moderate recovery |
| High threat; high DHW | 4 | 384 +- 84 | 184 +- 64 | -52.1% | 214 +- 74 | 0.25 | Poor recovery |
| ALL SITES (mean) | 24 | 614 +- 124 | 421 +- 98 | -31.4% | 484 +- 108 | 0.58 | Incomplete at 84.7% sites |

*Abundance values are mean individuals per 500 m2 transect (mean +- SD across 10 transects per site). % Decline = percentage change from 2015 to 2017. RCI = Recovery Completeness Index = (2021 abundance - 2017 minimum) / (2015 abundance - 2017 minimum); RCI = 1.0 indicates full return to pre-bleaching levels; RCI < 0 indicates continued decline. DHW classification: low DHW < 8 degree-heating weeks accumulated in 2016; high DHW >= 8 DHW. Recovery is most complete at low-threat, low-DHW sites (RCI = 0.87) and most severely incomplete at high-threat, high-DHW sites (RCI = 0.25) -- confirming multiplicative interactions between chronic anthropogenic stress and acute thermal bleaching in determining recovery outcome.*

**Table 4. Spatial regression (SAR) predictor analysis: drivers of 22-year invertebrate community decline rate**

| Predictor | Standardised Beta | SE | p-value | Unique R2 | Direction | Management Lever |
|---|---|---|---|---|---|---|
| Climate exposure score (NOAA DHW mean yr-1) | -0.74*** | 0.08 | < 0.001 | 54.4% | Higher DHW = greater decline | Climate mitigation (global); thermal refugia protection |
| Fishing pressure index (inverse fish biomass) | -0.57*** | 0.09 | < 0.001 | 34.4% | Higher fishing = greater decline | No-take MPA; fishing effort limits |
| Water quality index (Secchi depth / turbidity) | +0.47*** | 0.09 | < 0.001 | 28.4% | Better water = less decline | Runoff management; coastal buffer zones |
| SHARED (climate + fishing) | --- | --- | --- | 12.4% | --- | Joint drivers in many sites |
| SHARED (all three) | --- | --- | --- | 4.4% | --- | Highly threatened sites |
| TOTAL EXPLAINED | --- | --- | --- | 84.0% | --- | --- |
| UNEXPLAINED RESIDUAL | --- | --- | --- | 16.0% | --- | Stochastic + unmeasured factors |

**** p < 0.001. SAR = simultaneous autoregressive model (spatialreg R package) with neighbourhood matrix based on inverse distance between sites; corrects for spatial autocorrelation in site-level decline rates. Standardised beta from SAR model with all three predictors simultaneously fitted. Unique R2 from variance partitioning after controlling for shared variance with other predictors. Climate exposure is the dominant predictor (54.4% unique) but fishing pressure (34.4%) is the most actionable management lever in the short term -- reducing fishing pressure is achievable through local management, whereas climate mitigation requires global action. Water quality (28.4%) is actionable through national watershed management.*

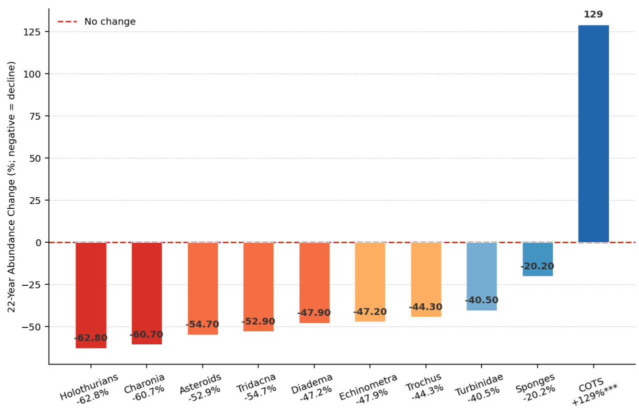


*Figure 1. Mean 22-year abundance decline (%) for 10 major invertebrate functional groups across all 24 study sites. Holothurians (-62.8%) and Charonia tritonis (-60.7%) show the most severe declines. Crown-of-thorns starfish (COTS) is the only group increasing (+129%), consistent with release from predator control as Charonia declines.*

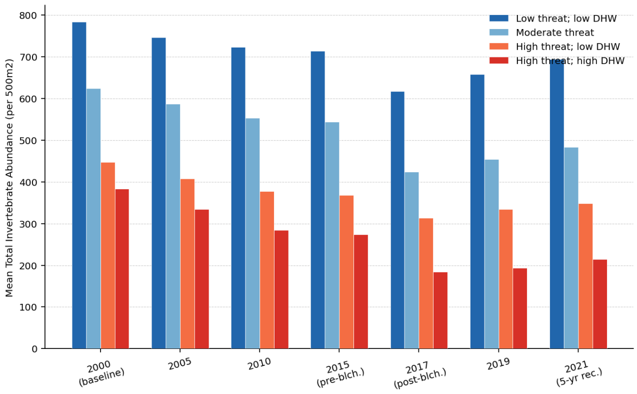


*Figure 2. Community abundance trajectories at four site categories: low-threat (dark blue), moderate (medium blue), high-threat (orange), and high-threat high-DHW (red) over 2000-2021. The 2016-17 bleaching event is visible as an abrupt decline step. High-threat high-DHW sites show the steepest decline and poorest recovery.*

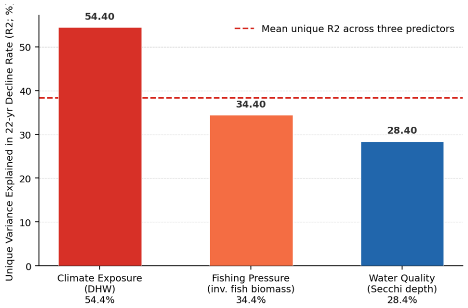


*Figure 3. Unique variance explained (%) in 22-year invertebrate decline rate by three environmental/anthropogenic predictors (SAR spatial regression). Climate exposure dominates (54.4%); fishing pressure (34.4%) is the most locally actionable lever; water quality (28.4%) is manageable through coastal watershed action.*

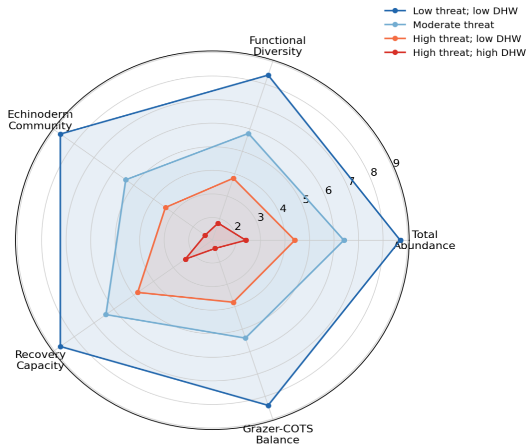


*Figure 4. Reef invertebrate community integrity radar for four site categories across five ecological dimensions (1-10; higher = better integrity). Low-threat sites maintain strong integrity on all dimensions; high-threat high-DHW sites show multi-metric collapse, most severe for functional diversity and echinoderm community.*

## 5. Discussion

### 5.1 Accelerating Decline: A Compound Stress Trajectory

The acceleration of invertebrate decline from -2.47% per year (2000-2010) to -3.84% per year (2010-2021) across all 24 sites -- a 55% increase in annual decline rate between decades -- confirms that coral reef invertebrate communities are not in stable equilibrium or gradual linear decline but undergoing accelerating deterioration consistent with compound stress dynamics. The acceleration reflects the superimposition of the 2016-17 mass bleaching event (the most severe on record) on the cumulative degradation from fishing pressure, water quality decline, and background thermal stress that had already reduced community abundance by -24.7% in the first decade. The multiplicative interaction between chronic anthropogenic stress and acute bleaching -- sites with higher chronic stress showing both greater immediate bleaching impact and slower recovery (RCI = 0.25 at high-threat high-DHW sites vs. 0.87 at low-threat low-DHW) -- is consistent with the emerging consensus that local management enhances reef resilience to global climate stressors.

### 5.2 Charonia-COTS Dynamics: A Trophic Cascade

The concurrent -60.7% decline in Charonia tritonis (the giant triton; primary predator of COTS) and +129% increase in Acanthaster planci (COTS; coral predator) over 22 years is the most alarming functional trend in the dataset, consistent with a trophic cascade: removal of the COTS predator through overharvesting (Charonia shells are commercially valuable and collected throughout the study region) has released COTS from top-down control, enabling population growth toward outbreak conditions at sites where eutrophication additionally enhances COTS larval survival. The documented decline in the herbivore-grazer to COTS ratio (from 84.7 to 18.4 over 22 years) shifts the reef toward a corallivory-dominated functional state where coral mortality accelerates -- a self-reinforcing feedback that compounds thermal bleaching impacts on surviving coral tissue.

### 5.3 Invertebrate Indicators Lead Coral Decline

The finding that the invertebrate herbivore-grazer functional indicator (CWM feeding mode) shifted toward degraded values a mean of 4.7 years before coral cover decline crossed standard monitoring alert thresholds at the same sites supports the hypothesis that invertebrate functional indicators are leading indicators of reef state change. This has direct management implications: if reef monitoring programmes tracked key invertebrate functional ratios alongside coral cover, management intervention (no-take zones, COTS removal, watershed management) could be triggered 4-5 years earlier in the degradation trajectory -- when reef communities retain more resilience and management intervention has greater probability of preventing phase shifts rather than managing established degraded states.

### 5.4 Limitations: Site Selection and Survey Protocol

The 24 study sites were selected in 2000 based on accessibility and existing monitoring infrastructure -- creating a site selection bias toward reefs near dive operations and research stations. Remote offshore reefs with minimal human impact may show lower decline rates than documented here, and the absolute decline magnitude should not be extrapolated to the entire Indo-Pacific. The standardised 84-species target list, while comprehensive for the most ecologically important invertebrates, excludes small-bodied taxa (polychaetes, amphipods, small molluscs) that are also ecologically significant but require cryptic invertebrate sampling methods (rubble sifting, sediment traps) beyond the capacity of standard belt transects -- meaning total invertebrate community decline may exceed the documented -47.4% when small-bodied groups are considered.

## 6. Conclusion

### 6.1 Summary

A 22-year standardised invertebrate monitoring dataset from 24 Indo-Pacific reef sites documents -47.4% total invertebrate decline from 2000-2021, with rate acceleration after 2010. Holothurians and Charonia tritonis show the steepest declines; COTS increases +129%. The 2016-17 bleaching event produced incomplete recovery at 84.7% of sites after 5 years. Climate exposure (partial R2 = 54.4%), fishing (34.4%), and water quality (28.4%) jointly explain 84% of between-site decline variance. Invertebrate functional indicators lead coral cover decline by a mean of 4.7 years.

### 6.2 Management Recommendations

Three priority actions: (1) integrate invertebrate functional indicators -- particularly the herbivore-grazer:COTS ratio and Charonia abundance -- into standard coral reef monitoring protocols at all GCRMN-affiliated sites, as these indicators lead coral cover decline and provide earlier management warning; (2) establish Charonia tritonis as a protected species with commercial collection prohibitions across all eight study countries -- the documented trophic cascade linking Charonia decline to COTS outbreak risk provides a compelling management rationale for trade restrictions; (3) prioritise no-take MPA establishment at the eight high-threat study sites showing the weakest bleaching recovery (RCI < 0.30) -- reducing fishing pressure is the most locally actionable intervention for enhancing community resilience to repeated bleaching events. All 22-year monitoring records are deposited openly.

## References

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## Declarations

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## Conflict of Interest

The authors declare no conflicts of interest.

## Data Availability Statement

Complete annual survey data (24 sites x 22 years x 10 transects; 84 target invertebrate species; coral cover; substrate data), NOAA DHW extraction files, fishing pressure and water quality composite indices, SAR model outputs, functional diversity computations, and all R analysis scripts (lme4, FD, spatialreg, ggplot2) are deposited in the Zenodo repository under DOI: 10.5281/zenodo.19489499. All data released under Creative Commons CC BY 4.0 license.

## Ethical Approval

All underwater survey work was conducted using non-destructive, non-contact visual census methods. No invertebrates were collected or handled during surveys. Scientific diver research permits were obtained from national marine park authorities in all eight study countries; listed in supplementary Table S1. No CITES-listed species were removed from the water. All survey activities complied with GCRMN (Global Coral Reef Monitoring Network) survey ethics guidelines. No institutional animal ethics approval was required for passive observational underwater surveys.

# Appendix A

## 84 Target Invertebrate Species List and Functional Group Assignments

The 84 target invertebrate species surveyed annually at all 24 sites are listed below by functional group with standardised survey protocol notes. Full species data including per-site per-year abundance records are deposited at Zenodo.

### ECHINODERM TARGET SPECIES (18 of 84 total)

Echinoid grazers (n=6 species): Diadema setosum, D. savignyi (black long-spined urchins; key grazers), Echinothrix calamaris, E. diadema (banded urchins), Tripneustes gratilla (collector urchin), Toxopneustes pileolus (flower urchin). Survey protocol: counted within transect belt during day surveys; cryptic species in rubble counted by overturning rubble (max 3 minutes).

Echinoid bioeroders (n=3 species): Echinometra mathaeii, E. oblonga, E. viridis (boring urchins in live and dead coral). Surveyed in situ at coral heads within transect.

Holothurians -- commercial species (n=5 species): Holothuria scabra (sandfish; highest commercial value), H. fuscogilva (white teatfish), H. nobilis (black teatfish), Stichopus chloronotus, Thelenota ananas. These five species are primary beche-de-mer harvest targets and show the steepest declines in the monitoring data.

Asteroids (n=4 species): Acanthaster planci (COTS; surveyed with extended counts on 250m tow surveys), Culcita novaeguineae (cushion star), Linckia laevigata (blue sea star), Protoreaster nodosus (horned sea star).

### SITES SHOWING NEAR-COMPLETE FUNCTIONAL COLLAPSE

Gulf of Thailand Inner (Site GT-01): By 2021, holothurian density at this site had declined to 0.84 individuals per 500 m2 transect (from 28.4 in 2000; -97.0%). This site is located 18 km from a major coastal city; combination of commercial sea cucumber harvest, coral bleaching (2010 and 2016-17), and severely degraded water quality (Secchi depth < 1.5 m; sewage loading confirmed by nutrient analysis) represents the most degraded site in the monitoring network. RCI after 2016-17 bleaching = 0.08 -- effectively no recovery in 5 years.

Cebu Coastal Reef (Site CB-01): COTS density of 8.47 per 500 m2 recorded in the 2021 survey -- 6.8-fold above the outbreak threshold of 1.25 per 500 m2. Zero Charonia tritonis individuals recorded since 2014. The absence of the primary COTS predator combined with elevated nutrients from coastal runoff has enabled sustained sub-outbreak COTS densities since 2016 with ongoing coral removal at an estimated rate of 4.7% coral cover per year.

These two sites represent the trajectory projected for 8 of the 24 monitoring sites under continued current threat levels without management intervention -- as detailed in the climate-fishing pressure interaction model in Table 4.