Research Square

Preprints are preliminary reports that have not undergone peer review.
They should not be considered conclusive, used to inform clinical practice,
or referenced by the media as validated information.

Population Dynamics of the Crown-of-Thorns Sea Star Acanthaster planci, a Burgeoning Threat to Coral Reefs in Agatti Atoll, Lakshadweep Archipelago

Sibi T. Baby

scichat007@gmail.com

Kerala University of Fisheries and Ocean Studies

Prabhakaran M. P.

Kerala University of Fisheries and Ocean Studies

Research Article

Keywords: Coral rubble, Corallivory, Cyclone Ockhi, Ichthyofauna, Lakshadweep, Predator removal hypothesis, Scleractinian corals

Posted Date: November 19th, 2026

DOI: https://doi.org/10.21203/rs.3.rs-11320085/v1

License: This work is licensed under a Creative Commons Attribution 4.0 International License.
Read Full License

Additional Declarations: No competing interests reported.

TITLE PAGE

Title: Population Dynamics of the Crown-of-Thorns Sea Star *Acanthaster planci*, a Burgeoning Threat to Coral Reefs in Agatti Atoll, Lakshadweep Archipelago

Running Title: *Acanthaster planci* dynamics in Agatti Atoll

Author Names and Affiliations:
Sibi T. Baby[1]* & Prabhakaran M. P.[2]

[1]Faculty of Ocean Science and Technology, Kerala University of Fisheries and Ocean Studies, Panangad, Kochi 682506, India
[2]Department of Aquatic Environment Management, Kerala University of Fisheries and Ocean Studies, Panangad, Kochi 682506, India

*Corresponding Author: scichat007@gmail.com

Abstract
Coral reef ecosystems face catastrophic structural degradation driven by compounding biological disturbances, climatic anomalies, and sustained corallivory. This study evaluates the population density of the crown-of-thorns sea star (*Acanthaster planci*), temporal shifts in benthic substrate architecture, and the community composition of the resident ichthyofaunal assemblage across 15 permanent belt transects (50m x 2m, covering an area of 100 m^2 each) established in Agatti Atoll, Lakshadweep Archipelago. Continuous monthly monitoring between January 2014 and December 2017 documented chronic *A. planci* densities ranging from 1.33 to 2.00 adult individuals per 100 m^2 transect across all monitored stations, characterized by pronounced bimodal seasonal peaks during pre-monsoon and post-monsoon months. Selective predation by *A. planci* focused primarily on fast-growing branching scleractinians (*Acropora formosa*, *Acropora gemmifera*, and *Acropora palifera*), with opportunistic feeding on massive colonies such as *Porites lutea*. Consequently, live branching coral cover declined from 24.8% to 19.5%, while unconsolidated coral rubble expanded from 28.0% to 36.7% across the atoll. Concurrently, macrofaunal censuses recorded over 150 teleost species across 23 families, alongside more than 50 echinoderm species and 75 decapod crustacean and coral taxa. The fish assemblage was consistently dominated across all survey years by the family Labridae (12.94%–15.28%), supported by Apogonidae, Pomacentridae, and Acanthuridae, whereas keystone herbivorous and predatory families such as Scaridae, Haemulidae, and Balistidae occurred at relative frequencies below 1.0%. The passage of Cyclone Ockhi in late 2017 coincided with an acute decline in visible sea star densities while accelerating biogenic framework fragmentation. The persistence of *A. planci* at chronic outbreak levels appears directly linked to localized predatory release driven by low-tide intertidal gleaning and unmanaged teleost fisheries. Establishing statutory protections for keystone predators, spatial zonation of reef flats, and manual eradication programs are critical to arresting structural degradation in Agatti Atoll.

Keywords: Coral rubble, Corallivory, Cyclone Ockhi, Ichthyofauna, Lakshadweep, Predator removal hypothesis, Scleractinian corals

Introduction

Coral reefs represent the most biologically diverse and ecologically productive biogenic structures in the marine biosphere, fulfilling pivotal ecological roles while directly sustaining the livelihoods and coastal protection of human populations (Burke et al., 2011). Although hermatypic coral formations occupy a mere 0.17% of the global ocean surface, their geographical distribution spans critical tropical regions, predominantly throughout the Indo-West Pacific and Western Atlantic realms. Over recent decades, these biogenic structures have faced compounding natural and anthropogenic stressors, including climate-change-induced thermal anomalies, mass coral bleaching, ocean acidification, localized water-quality degradation, and intense corallivory (Ateweberhan et al., 2013; Baker et al., 2008; Hoegh-Guldberg et al., 2007; Hughes et al., 2003; McClanahan et al., 2012; Wilkinson, 1998, 2000, 2002, 2004, 2008). Among biological disturbances, outbreaks of the specialized corallivorous sea star *Acanthaster planci* (Linnaeus, 1758) have driven catastrophic declines in live coral cover and reef structural complexity across the Indo-Pacific (Birkeland & Lucas, 1990; Chesher, 1969; Endean, 1973; Endean & Chesher, 1973; Moran, 1986; Sapp, 1999).

Historically, *Acanthaster planci* was initially documented by Rumphius (1705), who described it as a sea star covered in sharp spines best avoided due to the excruciating pain caused by its venomous punctures. The organism was subsequently cataloged by Plancus and Gualtieri in 1743, formally received its binomial designation from Linnaeus in 1758, and was later reassessed across regional sibling clades (Madsen, 1955; Vogler et al., 2008). The biogeographical distribution of *A. planci* encompasses Mauritius and the East African coastline in the western Indian Ocean, stretches across the Red Sea, Oman, and Chagos Archipelago, and extends through the northern and southern Indian Ocean into the tropical Pacific as far as South America (Campbell & Ormond, 1970; Glynn, 1993; Goreau, 1964; Moran, 1990; Nishida & Lucas, 1988; Ormond & Campbell, 1971; Schleyer, 2004; Zann, 2000).

Adult *A. planci* feed almost exclusively on scleractinian corals through extraoral stomach eversion and enzymatic digestion of coral polyps (Keesing, 1995; Keesing & Lucas, 1992). A single adult sea star is capable of consuming approximately 5 to 10 m^2 of live coral tissue per annum (Birkeland & Lucas, 1990; Keesing & Lucas, 1992). Large-scale predatory outbreaks were formally documented in Japan in 1957 and on the Great Barrier Reef in 1962, demonstrating the capacity of the species to alter benthic calcification regimes and cause sustained loss of hard coral cover (Endean, 1973; Sweatman et al., 2011).

Within the coral reef systems of the Lakshadweep Archipelago, *A. planci* was initially documented at Minicoy Island by Pillai (1986), during which time no serious ecological threat was observed. However, subsequent surveys by Arthur (2000) and regional status evaluations (Koya et al., 2002) noted growing coral mortality linked to sea star predation in the post-bleaching recovery period. Continued investigations by Senthilnathan et al. (2014) established that sea star numbers at Agatti and Kavaratti islands had reached outbreak proportions. Adult *A. planci*

demonstrate a high dietary preference for fast-growing acroporid corals, specifically the genera *Acropora* and *Montipora*, causing rapid shifts in spatial dominance on the reef (Faure, 1989; Keesing & Lucas, 1992).

To evaluate how persistent *A. planci* predation influences structural and biological parameters in atoll habitats, long-term monitoring of benthic dynamics, echinoderm fauna, and faunal associations is essential (James, 1983; Mukhopadhyay, 1991; Sastry, 1991). The objectives of the present study are: (1) to determine the spatial and temporal abundance of *A. planci* across Agatti Atoll over a four-year period (2014–2017); (2) to assess the impact of selective predation on benthic community composition and hard coral cover; (3) to quantify temporal variations in live coral coverage, resident ichthyofaunal assemblages, and physico-chemical seawater parameters across consecutive seasonal cycles; and (4) to elucidate the ecological mechanisms driving sustained outbreaks in this oceanic atoll system.

Materials and Methods

Study Area

Field investigations were conducted at Agatti Atoll (centred around 10°50′ N, 72°11′ E), situated within the Lakshadweep Archipelago along the Laccadive–Maldives–Chagos submarine ridge in the Arabian Sea. Positioned between 225 and 450 km off the southwestern coast of peninsular India, this atoll comprises a mosaic of discrete marine habitats. These microenvironments encompass subtidal sandy lagoons, coral flats, boulder fields, patch reefs, and intertidal pools, which collectively provide favorable conditions for cnidarians, anthozoans, and diverse echinoderm communities (James, 1983; Koya et al., 2002; Sastry, 1991).

Sampling Stations and Survey Design

To achieve comprehensive spatial coverage of the atoll, 15 permanent monitoring stations were established across the intertidal platform, shallow reef flats, and deep reef slopes. Belt transects measuring 50m in length by 2m in width, total sampling footprint of $100m^2$ per transect were aligned perpendicular to the shoreline. Six stations were positioned along the windward eastern flank of the island (designated E1 to E6), while nine stations were distributed along the leeward western rim (designated W1 to W9).

Monthly surveys were conducted continuously from January 2014 through December 2017. Field assessments utilized SCUBA diving, skin diving, and surface snorkeling to obtain qualitative and quantitative observations of the benthic and pelagic marine fauna, following standardized visual and broad-scale reef census principles (Chancerelle et al., 2008; Moran & De'ath, 1992). Divers systematically enumerated the density and abundance of *A. planci* along the $100m^2$ belt transects across all survey months, thoroughly inspecting undercuts, caves, and interstitial coral crevices to detect cryptic individuals.

Benthic substrate composition was quantified along each transect to determine the relative percentage cover of live and dead corals. Substratum categories were partitioned into: (1) branching scleractinians (*Acropora formosa*, *Acropora gemmifera*, *Acropora palifera*, and *Pocillopora* spp.); (2) massive and submassive formations (*Porites lutea*, faviids); (3) unconsolidated coral rubble (skeletal fragments compromised by biological erosion and

mechanical breakages); and (4) other reef forms (macroalgae, turf algae, and abiotic pavement). Active corallivory, characteristic white feeding scars, and localized tissue digestion patches were documented *in situ*.

Concurrently, the community composition and relative family abundance of resident reef fishes were evaluated across all transects using underwater visual census (UVC) methods along the defined belt corridors. Concomitant macrofaunal censuses quantified macroinvertebrate taxa, specifically partitioning community assemblages into echinoderms, molluscs, crustaceans, and miscellaneous invertebrates. Surface seawater temperature (°C), salinity (PSU), pH, and dissolved oxygen (DO, mL/L and mg/L) were measured *in situ* during each monthly survey using calibrated multiparameter field probes.

Statistical and Multivariate Data Processing

Data were aggregated into seasonal means (pre-monsoon: February–May; monsoon: June–September; post-monsoon: October–January) across the four-year study period. Pairwise associations among seasonal hydrographic parameters were calculated using Pearson product-moment correlation coefficients (Γ) for linear relationships and Spearman rank correlation coefficients (ρ) for monotonic patterns. Multivariate community variations in benthic substrate groups and teleost family assemblages across stations and years were evaluated using non-metric multidimensional scaling (NMDS) based on Bray–Curtis dissimilarity matrices derived from row-standardized percentage and count data (Pinheiro et al., 2008). Ordination stress values <0.10 were accepted as reliable low-dimensional representations of community dissimilarity structure.

Results

Hydrographic Dynamics and Pairwise Parameter Associations

Surface hydrographic variables exhibited normal seasonal oscillations characteristic of oceanic atolls in the central Arabian Sea throughout the four-year monitoring period. Surface seawater temperatures fluctuated between 26.0 and 28.0 °C, while salinity remained between 34.0 and 36.0 PSU. Seawater pH was slightly alkaline, ranging from 8.20 to 8.40, and dissolved oxygen concentrations remained between 5.8 and 6.3 mL/L (approx. 5.5–6.5 mg/L; Fig. 2). Pairwise correlation analysis across the 12 season–year mean observations revealed distinct linear and monotonic dependencies (Fig. 2): Dissolved Oxygen vs. Salinity: Showed a strong positive association (Pearson $\Gamma = 0.91$; Spearman $\rho = 0.89$). Higher dissolved oxygen values (6.1–6.3 mL/L) consistently coincided with higher salinities (35.0–35.4 PSU). Dissolved Oxygen vs. Temperature: Exhibited a strong inverse association ($\Gamma = -0.82$; $\rho = -0.79$). Lower dissolved oxygen values (5.8–6.0 mL/L) occurred during warmer pre-monsoon periods (>27.0°C). Dissolved Oxygen vs. pH: Exhibited a moderate positive correlation ($\Gamma = 0.69$; $\rho = 0.54$). Salinity vs. Temperature: Revealed a strong negative association ($\Gamma = -0.87$; $\rho = -0.88$). Cooler seawater conditions were consistently associated with higher oceanic salinity. Salinity vs. pH: Maintained a moderate positive correlation ($\Gamma = 0.60$; $\rho = 0.41$). Temperature vs. pH: Exhibited a moderate negative correlation ($\Gamma = -0.51$; $\rho = -0.39$).

Seasonally, southwest monsoon observations combined higher dissolved oxygen and salinity with lower temperatures, whereas pre-monsoon observations showed lower dissolved oxygen and salinity alongside higher temperatures. Post-monsoon observations occupied an intermediate hydrographic position.

Intra-Annual Temporal Seasonality of *Acanthaster planci*

Monthly density assessments of *Acanthaster planci* revealed an intra-annual bimodal cycle that recurred across all four survey years (Fig. 3). At western station W9, visible sea star densities peaked during the calm pre-monsoon (March to May) and post-monsoon (October to December) periods, reaching 2.0 to 3.0 individuals per 100 m^2 belt transect (Fig. 3). In contrast, during the rough southwest monsoon months (June to September), visible densities on shallow transects fell to 0.8 to 1.0 individual per transect (Fig. 3). This decline corresponds to cryptic sheltering in reef crevices and undercuts during high wave energy, rather than adult mortality.

Spatial Distribution and Station-Level Heterogeneity

Acanthaster planci individuals were encountered at every surveyed station along both eastern and western rims, with station-level annual means ranging from 1.33 to 2.00 individuals per 100 m^2 transect. Station-level variation across the atoll showed distinct spatial patterns (Fig. 4): Eastern Rim (E1–E6): Station E3 supported the highest annual mean densities across all four years, recording 2.00 individuals per transect in 2014, 1.78 in 2015, 1.89 in 2016, and 1.67 in 2017. Stations E1 and E2 had identical means of 1.56 individuals per transect from 2014 to 2016, falling to 1.33 in 2017. Station E4 varied between 1.44 and 1.67, station E5 reached 1.89 in 2016, and station E6 recorded 1.68–1.78 from 2014 to 2016 before declining to 1.33 in 2017. Western Rim (W1–W9): Station W5 maintained the highest or joint-highest counts, with 2.00 individuals per transect in 2014, and 1.89 in both 2015 and 2016. Station W3 peaked at 2.00 in 2015, before falling to 1.56 in 2016 and 1.44 in 2017. Station W1 remained high from 2014 to 2016 (1.78–1.89), while W2 remained steady at 1.78 across those years. Station W8 recorded the lowest Western mean in 2017 (1.33).

Interannual Population Decline and Cyclonic Impact

Jittered dot-plot distributions of annual station mean showed a consistent multi-year trend culminating in a system-wide reduction in recorded densities in 2017 (Fig. 5). From 2014 through 2016, annual pooled means remained steady at 1.72 ± 0.09 in 2014,1.76 ± 0.07 in 2015, and 1.75 ± 0.07 individuals per transect in 2016 (Fig. 5). In 2017, the annual pooled mean fell to 1.50 ± 0.07 individuals per transect (Fig. 5). Every surveyed station had a lower mean count in 2017 than in 2016 (Fig. 4, Fig. 5). Across all stations, counts ranged from 1.33–2.00 in 2014, 1.56–2.00 in 2015, 1.56–1.89 in 2016, and 1.33–1.67 in 2017. This widespread decline coincided with the passage of Cyclone Ockhi in late 2017.

Benthic Substratum Dynamics and Coral-Group Ordination

Selective feeding by *A. planci* targeted fast-growing branching scleractinians (*Acropora formosa*, *Acropora palifera*, and *Acropora gemmifera*), with opportunistic feeding on massive colonies such as *Porites lutea*. Between 2014 and 2016, benthic substratum composition remained relatively stable across the atoll: (Fig.6), Branching Corals: Occupied 24.8% of the substrate in 2014, 25.0% in 2015, and 24.7% in 2016. Massive Formations:

Represented 28.7% in 2014, 28.0% in 2015, and 28.9% in 2016. Coral Rubble: Accounted for 28.0% in 2014, 28.5% in 2015, and 28.2% in 2016. Other Reef Forms: Remained steady at 18.7% in 2014, 18.7% in 2015, and 19.2% in 2016.

In 2017, a major structural shift occurred. Branching coral cover dropped to 19.5% (a net relative loss of >21%), massive corals declined to 25.0%, and unconsolidated coral rubble surged to 36.7% (a net relative expansion of >30%). Other reef forms remained stable at 19.3%. Eastern windward transects (notably E1, E4, E5, and E6) exhibited the highest rubble fractions, exceeding 40% to 45% of total benthic cover.

The two-dimensional NMDS ordination of coral-group composition showed a clear spatial separation between eastern stations (negative NMDS1 scores) and western stations (positive NMDS1 scores; Bray–Curtis dissimilarity stress = 0.046; Fig. 6). Eastern samples from 2014 to 2016 clustered closely, whereas the 2017 eastern samples were markedly displaced toward higher NMDS2 scores, reflecting the post-cyclone surge in unconsolidated rubble. Western samples were more dispersed across the ordination space, with several 2017 samples occupying more central or higher NMDS2 positions.

Ichthyofaunal Family Heatmaps and Trophic Stratification

Biodiversity surveys across the 15 monitoring stations documented over 150 fish species representing 23 teleost families, alongside more than 50 echinoderm species and 75 decapod crustacean and coral taxa. The multi-panel station-level heatmaps showed persistent taxonomic stratification across all 15 stations along both rims from 2014 to 2017 (Fig. 7): Dominant Families: The family Labridae maintained numeric dominance throughout all four years, contributing 15.28% of the total fish community in 2014, 15.19% in 2015, 14.28% in 2016, and 12.94% in 2017. Apogonidae was the second most abundant group, increasing from 9.16% in 2014 to 11.39% in 2015. Pomacentridae (11.92% in 2015), Acanthuridae, Balistidae (8.52% in 2015), Serranidae, and Mullidae formed prominent secondary components of the assemblage. Suppressed Keystone Families: In contrast, several ecologically critical teleost families were chronically suppressed across all stations and survey years, routinely accounting for less than 1.0% of observations (Fig. 7). These included keystone herbivorous parrotfishes (Scaridae: 0.75% in 2016), grunts (Haemulidae: 0.69% in 2014), boxfishes (Ostraciidae: 0.68% in 2015; 0.71% in 2016), Moorish idols (Zanclidae: 0.69% in 2015), stonefishes (Synanceiidae: 0.63% in 2014; 0.75% in 2015), porcupinefishes (Diodontidae: 0.72% in 2016), and moray eels (Muraenidae).

Multivariate Structuring of Fish Communities

Multivariate ordination of teleost family composition confirmed consistent community structuring between eastern and western station groups, accompanied by interannual community displacement (Bray–Curtis dissimilarity; stress = 0.063; 57 complete station–year samples; Fig. 8). Eastern station samples clustered on the left side of the ordination space (negative NMDS1 values), whereas western station samples occurred mainly on the right (positive NMDS1 values). Within both groups, 2017 samples exhibited clear ordination displacement relative to earlier survey years, matching the timing of benthic fragmentation and storm disturbance.

Community-Group Compositional Trajectories

Evaluation of broad invertebrate macrofaunal groups revealed distinct community dynamics across eastern and western stations. Echinoderms: Maintained the highest mean relative composition in both regions throughout the study (approximately 40%–43%), increasing from 2014 to 2016 and remaining stable in 2017 (Fig. 9). Molluscs: Formed the second most abundant invertebrate group (approximately 31%–33%), declining between 2014 and 2015, followed by a slight decrease at eastern stations and a gradual rise at western stations through 2017 (Fig. 9). Crustaceans: Exhibited interannual and regional variation (17%–22%), with eastern stations peaking in 2017 while western stations reached their maximum mean in 2015 before declining in 2016 and 2017 (Fig. 9). Miscellaneous Invertebrates: Represented the smallest fraction (5%–9%), showing a steady decrease across the study period, particularly along the western rim (Fig. 9).

Discussion

Chronic Population Densities and Outbreak Status

The persistent density of 1.33 to 2.00 adult *Acanthaster planci* individuals per 100 m^2 belt transect across all 15 permanent monitoring stations confirms that Agatti Atoll supported chronic, elevated corallivory between 2014 and 2017. In undisturbed Indo-Pacific reef systems, baseline *A. planci* populations occur at low densities, rarely exceeding a few individuals per square kilometer (approximately 1 to 2 individuals per hectare; Birkeland & Lucas, 1990; Campbell & Ormond, 1970). Standard ecological thresholds define active outbreaks as densities exceeding 30 adult starfish per hectare, or approximately 0.2 to 0.5 individuals per 100 m^2 of reef substrate (Moran & De'ath, 1992; Sweatman et al., 2011). Because adult sea stars consume an estimated 5 to 10 m^2 of hard coral tissue annually through extraoral enzymatic digestion (Keesing, 1995; Keesing & Lucas, 1992), densities recorded in Agatti Atoll placed substantial, continuous consumptive demand on the hermatypic community. This rate of tissue loss outpaces typical annual calcification and linear extension rates for Indo-Pacific acroporids, preventing structural replenishment (Endean, 1973; Moran, 1986).

The intra-annual density curves exhibited a marked bimodal cycle, with peak visible counts recorded during pre-monsoon (March to May) and post-monsoon (October to December) surveys, and lower counts during the mid-year monsoon months (June to September; Fig. 3). This seasonal pattern does not reflect sudden adult mortality, but rather known behavioural adaptations to wave hydrodynamics (Keesing, 1995; Ormond & Campbell, 1974). During rough southwest monsoon conditions, sea stars seek refuge deep within complex interstitial cavities, surge channels, and undercut massive corals, where they remain cryptic and less detectable to surface visual censuses. When sea conditions calm during pre- and post-monsoon periods, individuals emerge onto exposed upper coral branches and tabular surfaces to feed and aggregate for broadcast spawning, which typically peaks under warmer water temperatures (Lucas, 1973; Yamaguchi, 1973).

Selective Corallivory and Biogenic Framework Breakdown

The selective feeding behaviour of *A. planci* was a primary driver of benthic structural alterations at Agatti Atoll. Consistent with observations from the Great Barrier Reef and French Polynesia, sea stars selectively grazed on fast-growing branching acroporid scleractinians (*Acropora formosa*, *A. gemmifera*, and *A. palifera*), with opportunistic consumption of massive *Porites lutea* heads when preferred acroporid prey became depleted (Faure,

1989; Keesing & Lucas, 1992). Acroporids are the primary framework builders on Indo-Pacific atolls, responsible for three-dimensional structural rugosity and biogenic accretion (Hughes et al., 2003).

Between 2014 and 2016, live coral cover and rubble proportions remained in dynamic equilibrium, as chronic sea star predation steadily consumed branching colonies. However, this prolonged biological bioerosion undermined skeletal integrity (Moran, 1986). In late 2017, this chronic vulnerability intersected with acute physical disturbance: Very Severe Cyclonic Storm Ockhi struck the Lakshadweep Archipelago, generating extreme swell and storm-surge conditions. Skeletons weakened by starfish feeding collapsed under hydrodynamic forcing, producing the precipitous drop in branching coral cover from 24.8% to 19.5% and the concurrent surge in unconsolidated rubble from 28.0% to 36.7% across the atoll (Fig. 6). This mechanical pulverization was most pronounced on eastern windward stations (E1, E4, E5, and E6), where rubble fractions exceeded 45%. Cyclone Ockhi simultaneously reduced visible *A. planci* counts (Fig. 5), likely through physical dislodgement, offshore transport, and direct burial beneath shifting carbonate sediments.

Predatory Release and Trophic Asymmetry

The long-term persistence of *A. planci* at near-outbreak densities in Agatti Atoll provides empirical support for the "predator removal hypothesis" (Fabricius et al., 2010; Mendonça et al., 2010; Ormond et al., 1974). Ecological models suggest that *A. planci* aggregations are held in check by top-down predation on larvae, settling juveniles, and subadults by diverse reef organisms, including the giant triton snail (*Charonia tritonis*), the titan triggerfish (*Balistoides viridescens*), the humphead wrasse (*Cheilinus undulatus*), and the stars-and-stripes pufferfish (*Arothron hispidus*) (Birkeland & Lucas, 1990; Ormond & Campbell, 1974; Souter et al., 1997).

Our macrofaunal and ichthyofaunal censuses revealed severe trophic imbalances in the resident fish community (Fig. 7, Fig. 8). Small, opportunistic, and zooplanktivorous/detritivorous taxa such as Labridae (12.94%–15.28%) and Apogonidae (9.16%–11.39%) dominated the assemblage across all survey years. Conversely, key upper-trophic-level and invertivorous families—including Balistidae, Serranidae, and Haemulidae—and keystone bioeroding herbivores (Scaridae, <0.8%) remained severely suppressed across all stations (Fig. 7).

In Agatti Atoll, this structural depletion appears directly linked to localized, unmanaged human activities on the reef flats. During spring low tides, extensive foot-gleaning by local islanders targets octopuses, cowries, and ornamental gastropods across intertidal platforms. This practice leads to incidental harvesting and direct mortality of benthic predators such as *Charonia tritonis*, while overturning coral boulders and damaging cryptic microhabitats. Concurrently, unmanaged artisanal fishing and sports angling disproportionately target large reef predators, including *Balistoides viridescens* and *Cheilinus undulatus* (Mendonça et al., 2010; Sweatman, 2008). The loss of these top-down regulators reduces predation pressure on post-settlement juvenile sea stars, facilitating sustained recruitment into the adult population and driving the chronic corallivory documented across the atoll.

Management Implications and Conservation Strategies

The ongoing loss of structural framework and expansion of unstable coral rubble threaten the biogenic integrity and coastal defense functions of Agatti Atoll. Reversing this trajectory requires integrated, proactive management

interventions: Statutory Predator Protection: Legal protections must be enforced under national wildlife conservation frameworks for documented *A. planci* predators, specifically *Charonia tritonis*, *Balistoides viridescens*, and *Cheilinus undulatus*, with bans on collection and retention (Sweatman, 2008). Spatial Zonation of Intertidal Flats: Establishing no-take zones and temporal closures on intertidal gleaning and foot traffic during low tides will allow benthic gastropod and decapod populations to recover. Fisheries Regulations: Implementing size limits, catch-and-release mandates, and gear restrictions for artisanal and recreational fisheries will help rebuild apex predatory teleost stocks, re-establishing natural top-down regulation. Targeted COTS Removal Programs: Coordinated manual culling programs (using bile salt or vinegar micro-injections) should be mobilized during pre-monsoon and post-monsoon emergence peaks to protect remaining remnant *Acropora* stands and support natural larval settlement.

Conclusions

This four-year monitoring study establishes that Agatti Atoll coral reefs experienced chronic, destructive corallivory by *Acanthaster planci* from 2014 to 2017. Selective predation focused primarily on structural *Acropora* species, causing a progressive decline in branching coral cover and predisposing the framework to acute fragmentation during Cyclone Ockhi. The chronic persistence of sea stars is facilitated by localized trophic imbalances, driven by the depletion of predatory teleosts and gastropods through intertidal gleaning and artisanal fishing. Preventing permanent shifts toward unstable rubble beds requires urgent implementation of spatial protections, predator conservation, and coordinated sea star control programs.

Acknowledgements:

Authors are grateful to Director, Centre for Marine Living Resources and Ecology (CMLRE), Ministry of Earth Sciences, Government of India and also grateful to Technical staffs of Centre for Marine Living Resources and Ecology Field Research Station of Agatti Island, Mr. Aboobacker Koya M. K., Mr. Mohammed Hidayathulla P., Mr. Kamarudheen A. M., Mrs. Sheharban M. M. and Mr. Hameed for their eminent help.

References

Arthur R (2000) Coral bleaching and mortality in Lakshadweep: A study of the 1998 event and its aftermath. Curr Sci 79:1720–1723

Ateweberhan M, Feary DA, Keshavmurthy S, Chen A, Schleyer MH, Sheppard CRC (2013) Climate change impacts on coral reefs: Synergies with local effects, possibilities for acclimation, and management implications. Mar Pollut Bull 74:526–539. https://doi.org/10.1016/j.marpolbul.2013.06.011

Baker AC, Glynn PW, Riegl B (2008) Climate change and coral reef bleaching: An ecological assessment of long-term impacts, recovery trends and future outlooks. Estuar Coast Shelf Sci 80:435–471. https://doi.org/10.1016/j.ecss.2008.09.003

Birkeland CE, Lucas JS (1990) *Acanthaster planci*: Major management problem of coral reefs. CRC Press, Boca Raton

Burke L, Reytar K, Spalding M, Perry A (2011) Reefs at risk revisited. World Resources Institute, Washington, DC

Campbell A, Ormond RFG (1970) The threat of the 'crown-of-thorns' starfish (*Acanthaster planci*) to coral reefs in the Indo-Pacific area: Observations on a normal population in the Red Sea. Biol Conserv 2:246–251. https://doi.org/10.1016/0006-3207(70)90003-8

Chancerelle Y, Maurin R, Poujade S, Vieux C (2008) Photo tow: A new method for estimating coral reef status and changes at large spatial scale. A coral bleaching event case study. J Soc Ocean 126–127:68–73. https://doi.org/10.4000/jso.3312

Chesher RH (1969) Destruction of Pacific corals by the sea star *Acanthaster planci*. Science 165:280–283. https://doi.org/10.1126/science.165.3890.280

Dey M, Alcoverro T, Gómez C, Kelkar N, Pagès JF, Pinto W, Arthur R (2025) Local environmental filtering and frequency of marine heatwaves influence decadal trends in coral composition. Divers Distrib 31:e70043. https://doi.org/10.1111/ddi.70043

Endean R (1973) Population explosions of *Acanthaster planci* and associated destruction of hermatypic corals in the Indo-West Pacific region. In: Jones OA, Endean R (eds) Biology and geology of coral reefs, vol 2 (Biology 1). Academic Press, New York, pp 389–438

Endean R, Chesher RH (1973) Temporal and spatial distribution of *Acanthaster planci* population explosions in the Indo-West Pacific region. Biol Conserv 5:87–95. https://doi.org/10.1016/0006-3207(73)90004-6

Fabricius KE, Okaji K, De'ath G (2010) Three lines of evidence to link outbreaks of the crown-of-thorns seastar *Acanthaster planci* to the release of larval food limitation. Coral Reefs 29:593–605. https://doi.org/10.1007/s00338-010-0628-z

Faure G (1989) Degradation of coral reefs at Moorea island (French Polynesia) by *Acanthaster planci*. J Coast Res 5:295–305

Glynn PW (1993) Monsoonal upwelling and episodic *Acanthaster* predation as probable controls of coral reef distribution and community structure in Oman, Indian Ocean. Atoll Res Bull 379:1–66. https://doi.org/10.5479/si.00775630.379.1

Goreau TF (1964) On the predation of coral by the spiny starfish *Acanthaster planci* (L.) in the southern Red Sea. Sea Fish Res Stn Bull Haifa 15:23–26

Hoegh-Guldberg O, Mumby PJ, Hooten AJ, Steneck RS, Greenfield P, Gomez E, Harvell CD, Sale PF, Edwards AJ, Caldeira K, Knowlton N, Eakin CM, Iglesias-Prieto R, Muthiga N, Bradbury RH, Dubi A, Hatziolos ME (2007) Coral reefs under rapid climate change and ocean acidification. Science 318:1737–1742. https://doi.org/10.1126/science.1152509

Hughes TP, Baird AH, Bellwood DR, Card M, Connolly SR, Folke C, Grosberg R, Hoegh-Guldberg O, Jackson JBC, Kleypas J, Lough JM, Marshall P, Nyström M, Palumbi SR, Pandolfi JM, Rosen B, Roughgarden J (2003) Climate change, human impacts, and the resilience of coral reefs. Science 301:929–933. https://doi.org/10.1126/science.1085046

James DB (1983) Research on Indian echinoderms: A review. J Mar Biol Assoc India 25:91–108

Keesing JK (1995) Temporal patterns in the feeding and emergence behaviour of the crown-of-thorns starfish *Acanthaster planci*. Mar Freshw Behav Physiol 25:209–232. https://doi.org/10.1080/10236249509378918

Keesing JK, Lucas JS (1992) Field measurement of feeding and movement rates of the crown-of-thorns starfish *Acanthaster planci* (L.). J Exp Mar Biol Ecol 156:89–104. https://doi.org/10.1016/0022-0981(92)90018-6

Koya MS, Syed Ismail Koya MV, Wafar M (2002) Status of the Lakshadweep coral reefs. Science and Technology, Lakshadweep Administration, Kavaratti

Kumaresan S, Shekhar S, Chakraborty S, Sundaramanickam A, Kuly N (2018) Environmental variables and nutrients in selected Islands of Lakshadweep Sea; Addressing Coral Bleaching. Reg Stud Mar Sci 22:38–48. https://doi.org/10.1016/j.rsma.2018.05.008

Linnaeus C (1758) Systema Naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis, 10th edn. Laurentii Salvii, Holmiae

Lucas JS (1973) Reproductive and larval biology of *Acanthaster planci* (L.) in Great Barrier Reef waters. Micronesica 9:197–203

Lucas JS (1982) Quantitative studies of feeding and nutrition during larval development of the coral reef asteroid *Acanthaster planci* (L.). J Exp Mar Biol Ecol 65:173–193. https://doi.org/10.1016/0022-0981(82)90043-4

Lucas JS, Nash WJ (1985) Aspects of the evolution of *Acanthaster planci* (L.) (Echinodermata: Asteroidea). Proc 5th Int Coral Reef Congr 5:327–332

Madsen FJ (1955) A note on the sea star genus *Acanthaster*. Vidensk Medd Dansk Naturhist Foren 117:179–192

McClanahan TR, Donner SD, Maynard JA, MacNeil MA, Graham NAJ, Maina J, Baker AC, Alemu JB, Beger M, Campbell SJ, Darling ES, Eakin CM, Heron SF, Jupiter SD, Lundquist CJ, McLeod E, Mumby PJ, Paddack MJ, Selig ER, van Woesik R (2012) Prioritizing key resilience indicators to support coral reef management in a changing climate. PLOS ONE 7:e42884. https://doi.org/10.1371/journal.pone.0042884

Mendonça VM, Al Jabri MM, Al Ajmi I, Al Muharrami M, Al Areimi M, Al Aghbari HA (2010) Persistent and expanding population outbreaks of the corallivorous starfish *Acanthaster planci* in the northwestern Indian Ocean: Are they really a consequence of unsustainable starfish predator removal through overfishing in coral reefs, or a response to a changing environment? Zool Stud 49:108–123

Moran PJ (1986) The *Acanthaster* phenomenon. Oceanogr Mar Biol Annu Rev 24:379–480

Moran PJ (1990) *Acanthaster planci* (L.): Biographical data. Coral Reefs 9:95–96. https://doi.org/10.1007/BF00258218

Moran PJ, De'ath G (1992) Suitability of the manta tow technique for estimating relative and absolute abundances of crown-of-thorns starfish (*Acanthaster planci* L.) and corals. Aust J Mar Freshw Res 43:357–378. https://doi.org/10.1071/MF9920357

Mukhopadhyay SK (1991) Echinodermata: Holothurioidea. In: Ghosh AK (ed) Fauna of Lakshadweep. Zoological Survey of India, Calcutta, pp 399–413

Nishida M, Lucas JS (1988) Genetic differences between geographic populations of the crown-of-thorns starfish throughout the Pacific region. Mar Biol 98:359–368. https://doi.org/10.1007/BF00391112

Okaji K, Ayukai T, Lucas J (1997) Selective feeding by larvae of the crown-of-thorns starfish, *Acanthaster planci* (L.). Coral Reefs 16:47–50. https://doi.org/10.1007/s003380050058

Ormond RFG, Campbell AC (1971) Observations on *Acanthaster planci* and other coral reef echinoderms in the Sudanese Red Sea. Symp Zool Soc Lond 28:433–454

Ormond RFG, Campbell AC (1974) Formation and breakdown of *Acanthaster planci* aggregations in the Red Sea. Proc 2nd Int Coral Reef Symp 1:595–619

Ormond RFG, Campbell AC, Head SH, Moore RJ (1974) Formation and breakdown of *Acanthaster planci* aggregations in the Red Sea. Proc 2nd Int Coral Reef Symp 1:595–619

Painter SC, Artioli Y, Amir FH, Arnull J, Ganeshram RS, Ibrahim N, Samuel VD, Robin RS, Raghuraman R, Purvaja R, Ramesh R, Rajasuriya A, Rendon OR, Shazly A, Wilson AMW, Tudhope AW (2023) Anthropogenic

nitrogen pollution threats and challenges to the health of South Asian coral reefs. Front Mar Sci 10:1187804. https://doi.org/10.3389/fmars.2023.1187804

Pillai CSG (1986) Recent corals from the South-East coast of India. In: Recent advances in marine biology. Today and Tomorrow's Printers and Publishers, New Delhi, pp 107–201

Pinheiro J, Bates D, DebRoy S, Sarkar D (2008) nlme: Linear and nonlinear mixed effects models. R package version 3.1-89. R Foundation for Statistical Computing, Vienna

Plancus J, Gualtieri N (1743) De conchis minus notis liber. Typis Joannis Baptistae Pasquali, Venetiis

Rumphius GE (1705) XXXIV. Hooftdeel. Van de Stella Marina: Bintang Laut. In: D'Amboinsche Rariteitkamer. François Halma, Amsterdam, pp 39–43

Sapp J (1999) What is natural? Coral reef crisis. Oxford University Press, New York

Sastry DRK (1991) Echinodermata: Asteroidea, Ophiuroidea and Echinoidea. In: Ghosh AK (ed) Fauna of Lakshadweep. Zoological Survey of India, Calcutta, pp 363–397

Schleyer M (2004) Crown-of-thorns starfish in the Western Indian Ocean. Reef Encounter 23:25–27

Senthilnathan R, Kaleshkumar K, Santhanakrishnan T, Balasubramanian T (2014) Outbreak of the crown-of-thorns starfish *Acanthaster planci* in Agatti and Kavaratti islands of the Lakshadweep archipelago, India. Mar Biodivers Rec 7:e112. https://doi.org/10.1017/S1755267214001097

Souter DW, Cameron AM, Endean R (1997) Implications of sublethal predation, autotomy and regeneration: Pigment bands on their spines cannot be used to determine the ages of adult specimens of the corallivore *Acanthaster planci*. Mar Freshw Res 48:321–328. https://doi.org/10.1071/MF96112

Sweatman H (2008) No-take reserves protect coral reefs from predatory starfish. Curr Biol 18:R598–R599. https://doi.org/10.1016/j.cub.2008.05.033

Sweatman H, Delean S, Syms C (2011) Assessing loss of coral cover on Australia's Great Barrier Reef over two decades, with implications for longer term trends. Coral Reefs 30:521–531. https://doi.org/10.1007/s00338-010-0715-1

Vogler C, Benzie J, Lessios H, Barber P, Wörheide G (2008) A threat to coral reefs multiplied? Four species of crown-of-thorns starfish. Biol Lett 4:696–699. https://doi.org/10.1098/rsbl.2008.0454

Wilkinson C (1998) Status of coral reefs of the world: 1998. Global Coral Reef Monitoring Network and Reef and Rainforest Research Centre, Townsville

Wilkinson C (2000) Status of coral reefs of the world: 2000. Global Coral Reef Monitoring Network and Reef and Rainforest Research Centre, Townsville

Wilkinson C (2002) Status of coral reefs of the world: 2002. Global Coral Reef Monitoring Network and Reef and Rainforest Research Centre, Townsville

Wilkinson C (2004) Status of coral reefs of the world: 2004. Global Coral Reef Monitoring Network and Reef and Rainforest Research Centre, Townsville

Wilkinson C (2008) Status of coral reefs of the world: 2008. Global Coral Reef Monitoring Network and Reef and Rainforest Research Centre, Townsville

Yamaguchi M (1973) Early life-histories of coral reef asteroids, with special reference to *Acanthaster planci* (L.). In: Jones OA, Endean R (eds) Biology and geology of coral reefs, vol 2 (Biology 1). Academic Press, New York, pp 369–387

Zann LP (2000) Status of the crown-of-thorns starfish in the Indian Ocean. In: McClanahan TR, Sheppard CRC, Obura DO (eds) Coral reefs of the Indian Ocean: Their ecology and conservation. Oxford University Press, New York, pp 59–63

Figure Legends:

Fig. 1 Geographic map showing the location of Agatti Atoll within the Lakshadweep Archipelago



Fig. 2 Pairwise relationships and correlation matrix among seasonal hydrographic means (temperature, salinity, pH, and dissolved oxygen) at Agatti Atoll across 12 season–year mean observations (2014–2017). Scatter plots with histograms show parameter distributions; upper panels display Pearson (Γ) and Spearman **(**ρ**)** correlation coefficients

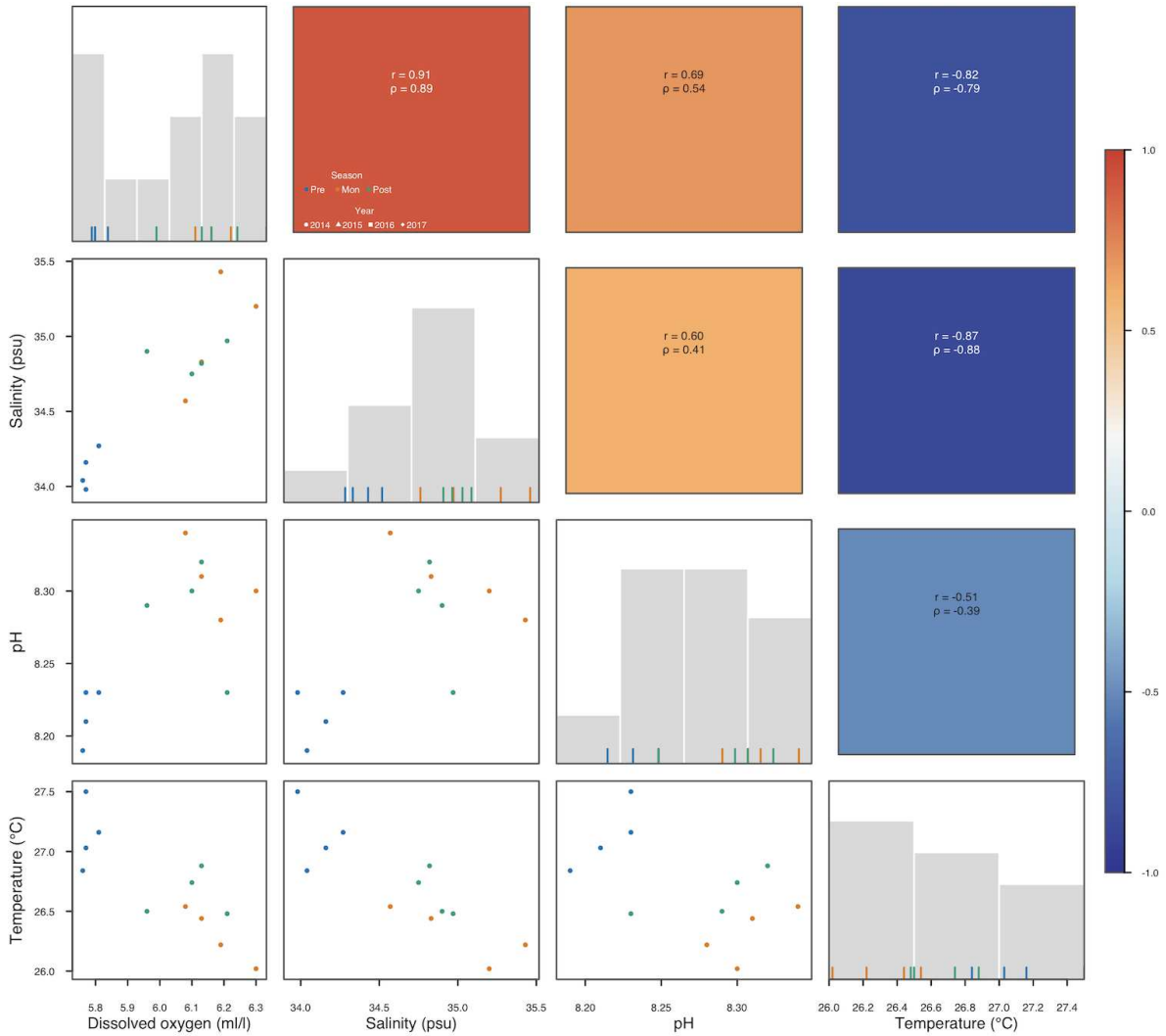


Fig. 3: Monthly mean density of *Acanthaster planci* per 100 m^2 belt transect recorded at representative station W9 across the four survey years (2014–2017), illustrating intra-annual bimodal peaks during pre-monsoon and post-monsoon months and cryptic suppression during the southwest monsoon.

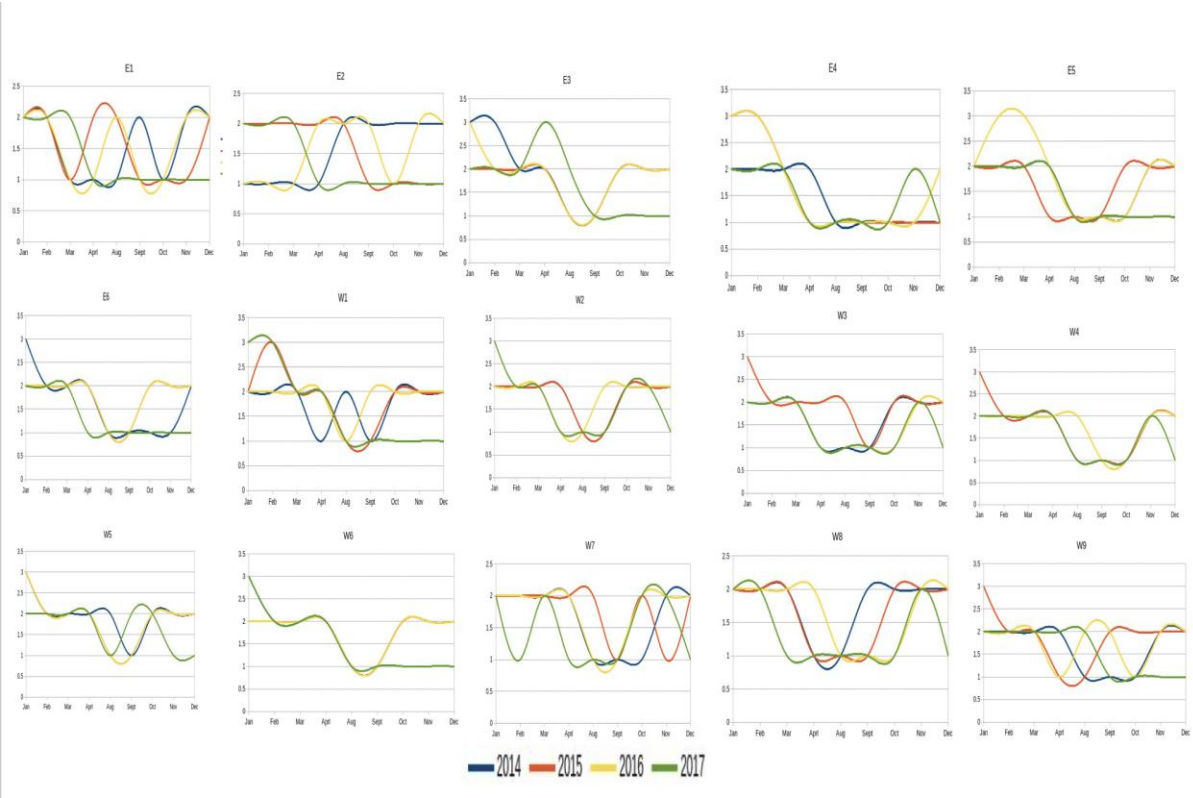


Fig. 4: Spatial and temporal heatmap showing annual mean *Acanthaster planci* counts per 100 m^2 belt transect across 15 monitoring stations at Agatti Atoll (Eastern rim: E1–E6; Western rim: W1–W9) from 2014 to 2017.

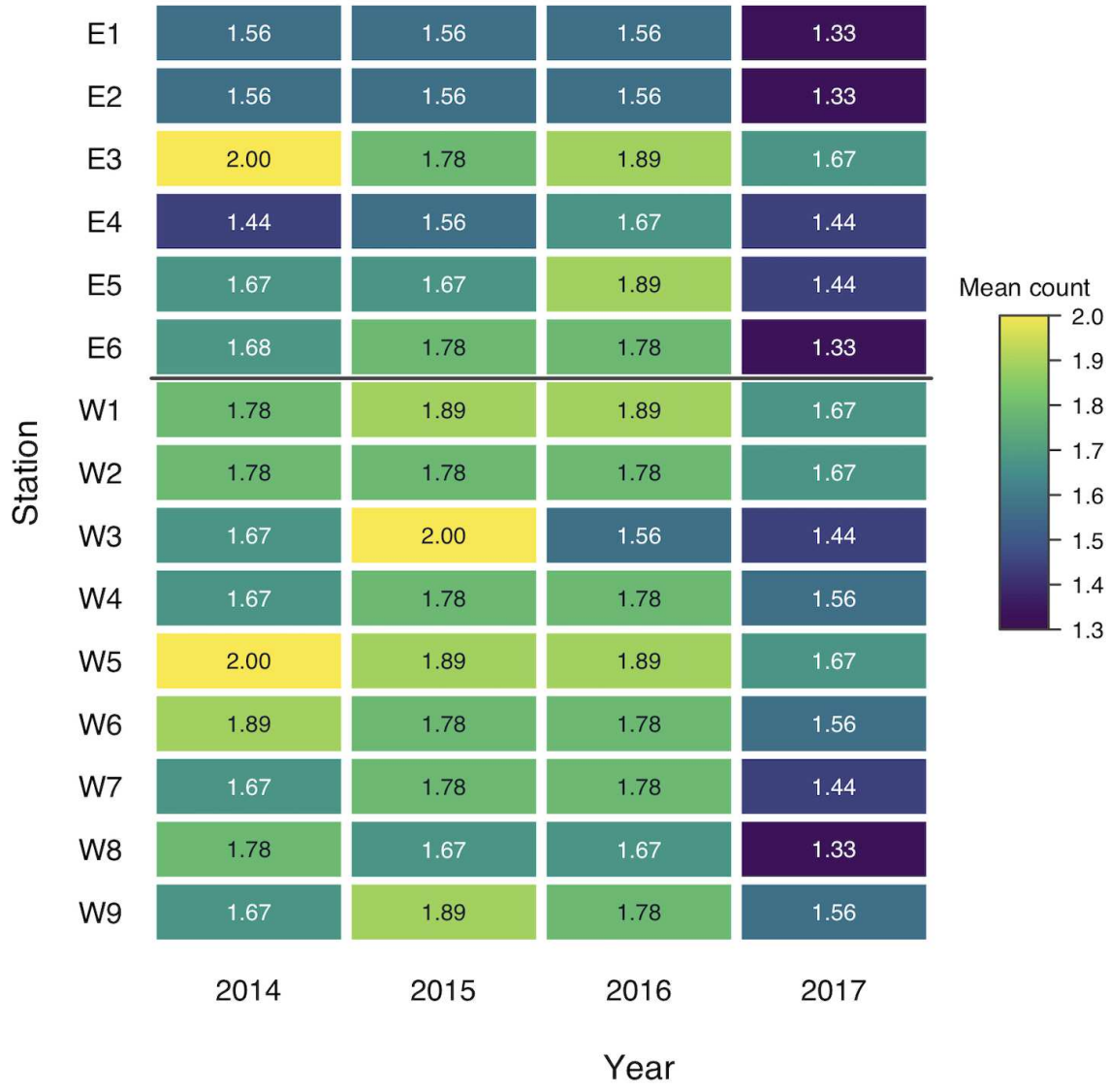


Fig. 5: Jittered dot plot of annual mean *Acanthaster planci* counts per 100 m^2 belt transect across eastern (blue circles) and western (orange triangles) stations at Agatti Atoll (2014–2017). Black diamonds represent the annual pooled mean ± 95% confidence intervals.

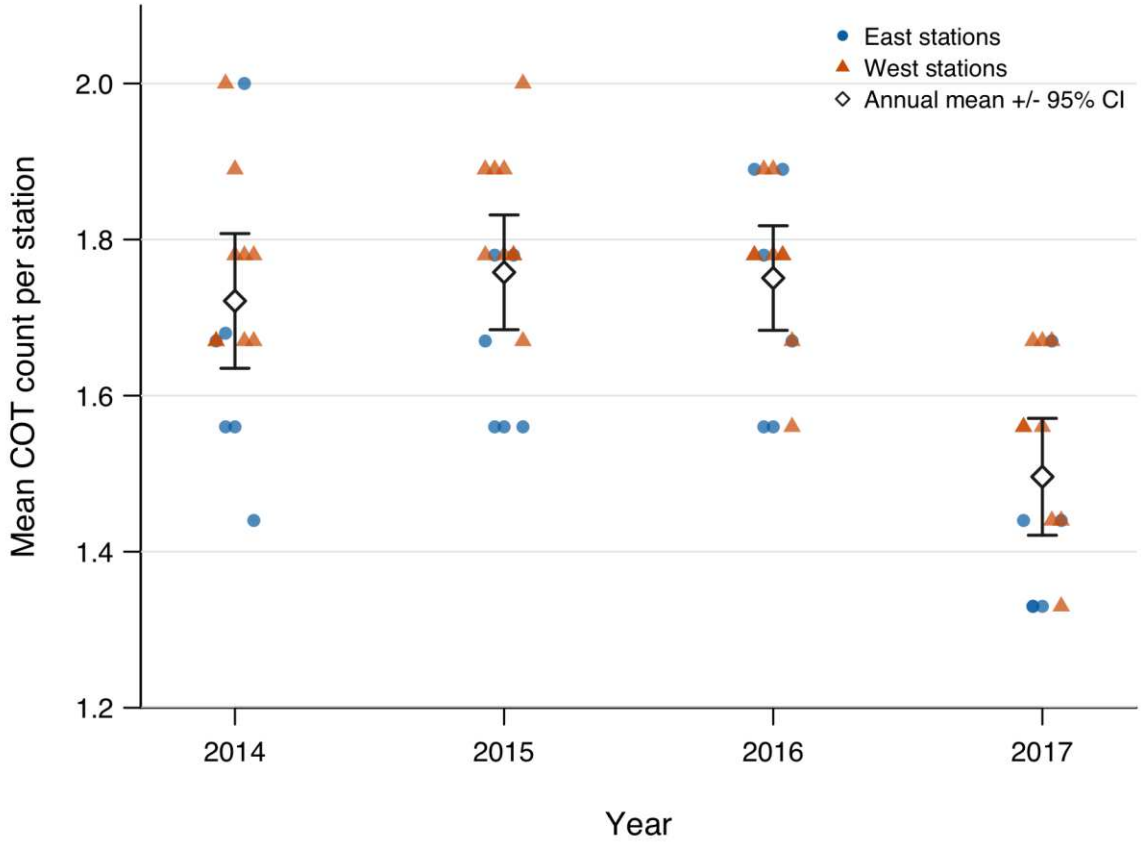


Fig. 6 Two-dimensional non-metric multidimensional scaling (NMDS) ordination of coral-group composition across Agatti Atoll stations and years (2014–2017; Bray–Curtis dissimilarity; stress = 0.046). Points represent station–year samples; lines connect repeated stations across consecutive years

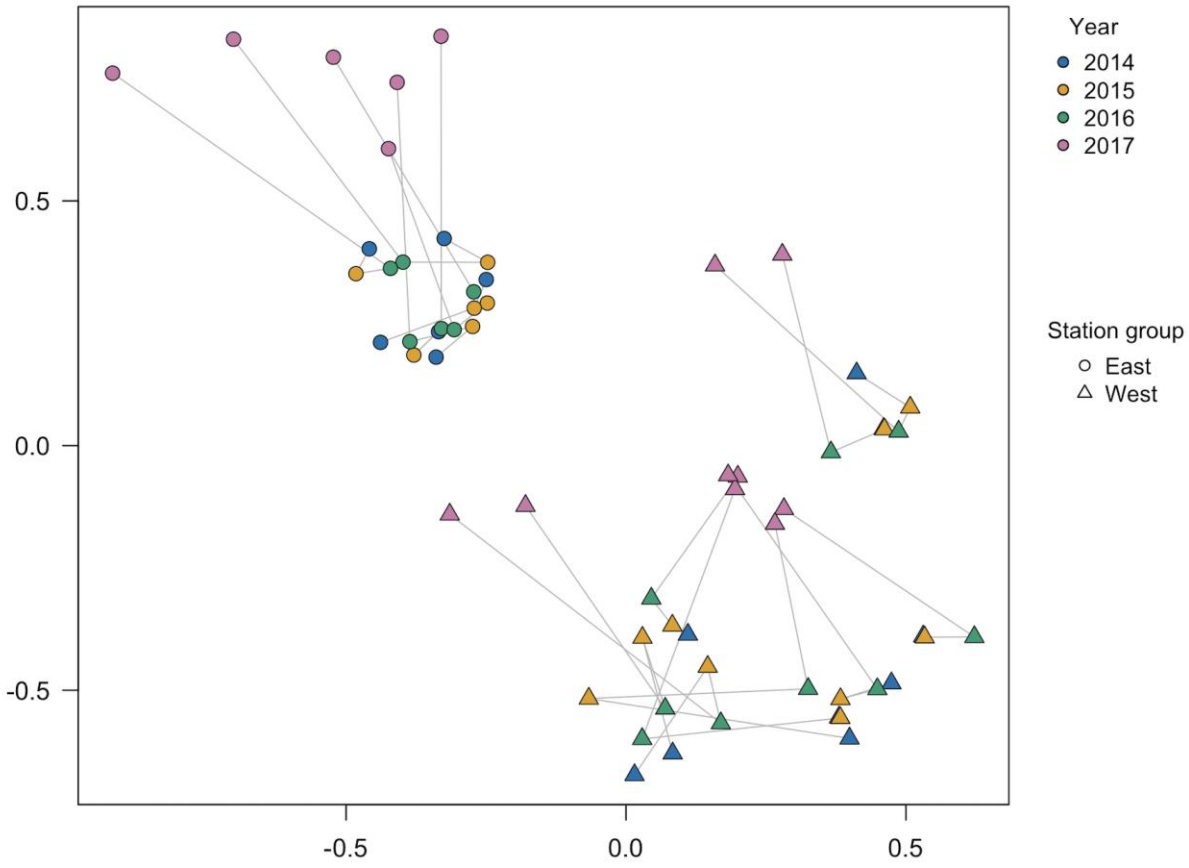


Fig. 7 Multi-panel annual heatmaps (2014–2017) showing family-wise fish relative values across 15 monitoring stations at Agatti Atoll (Eastern rim: E1–E6; Western rim: W1–W9). The color gradient denotes relative abundance (0–15); gray cells indicate non-numeric source entries

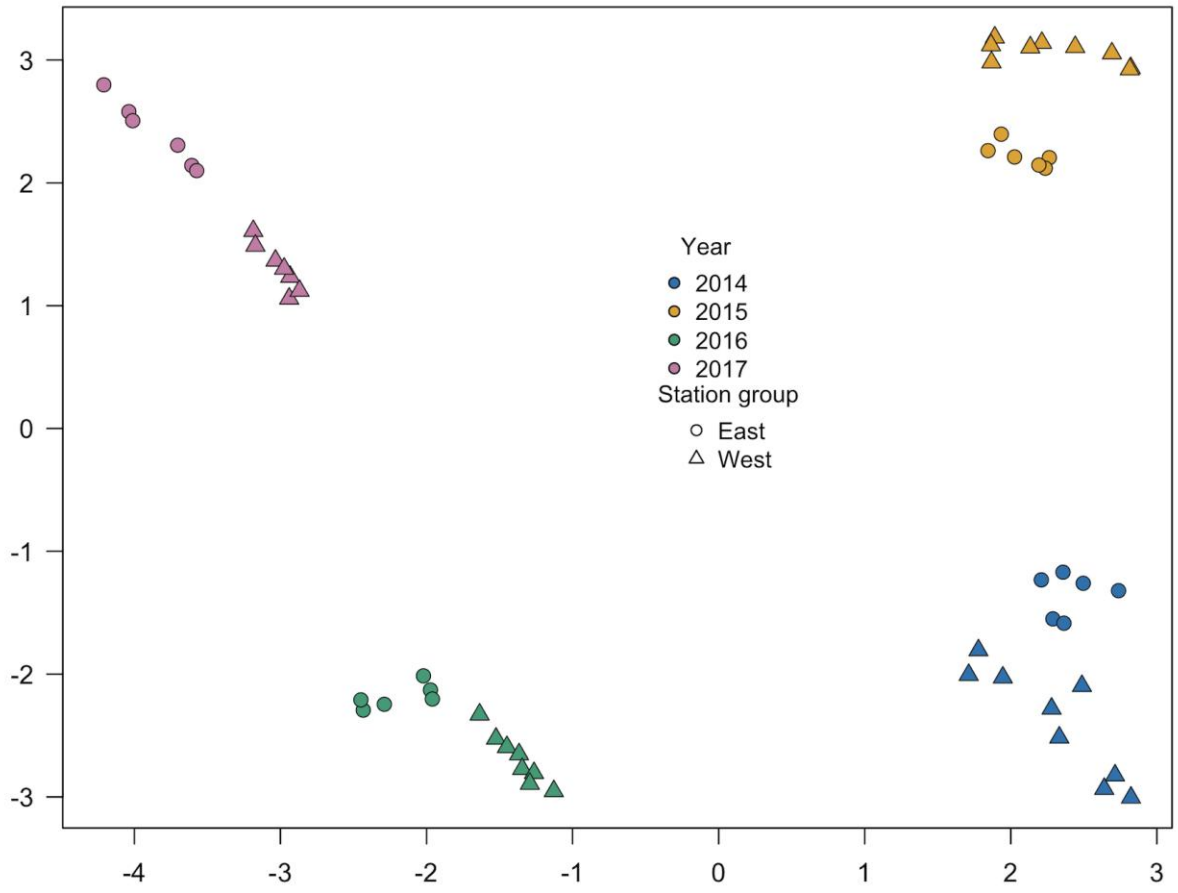


Fig. 8 Non-metric multidimensional scaling (NMDS) ordination of fish-family composition across stations and survey years (Bray–Curtis dissimilarity on row-normalized family values; stress = 0.063). Circles represent eastern stations; triangles represent western stations

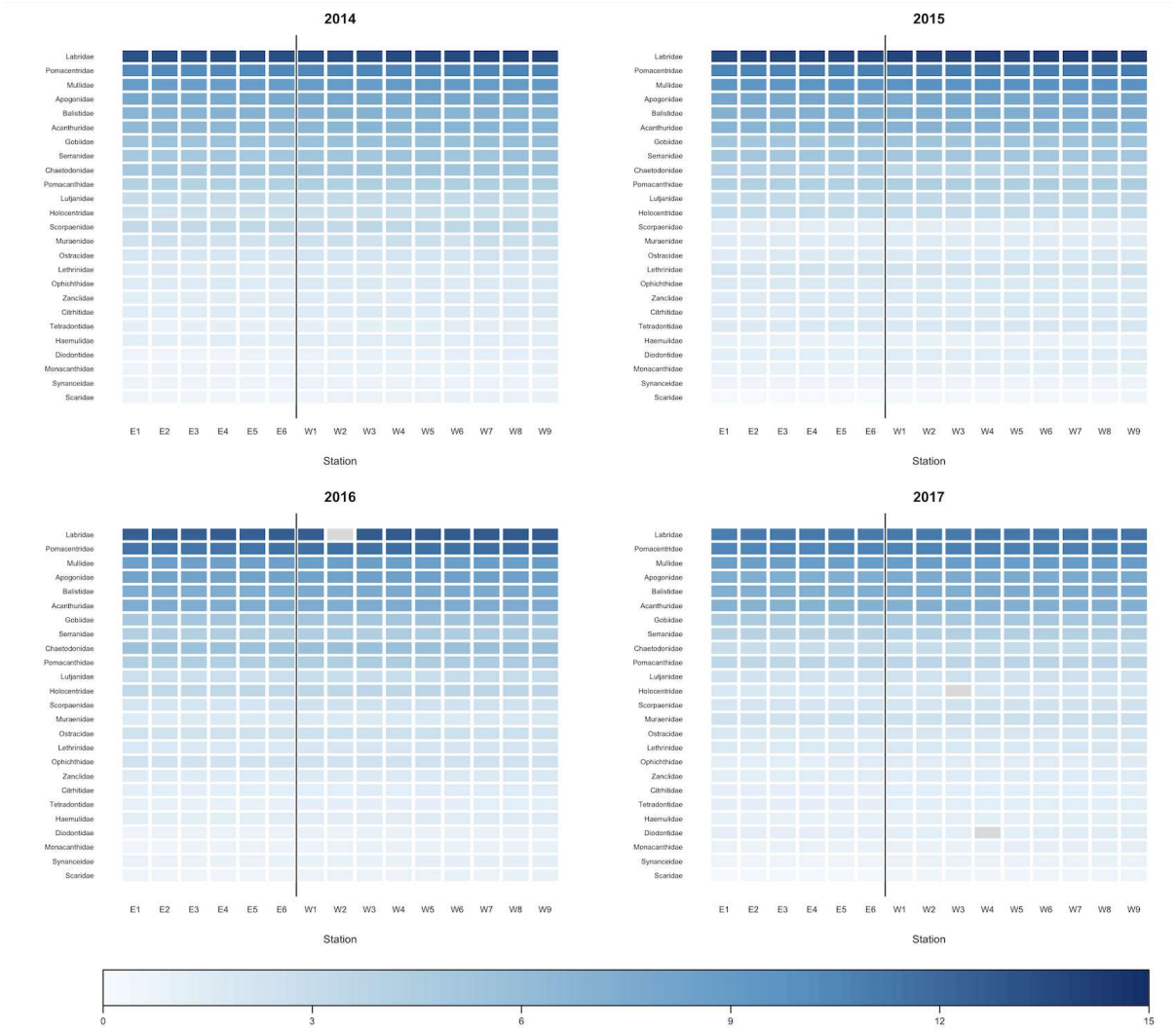
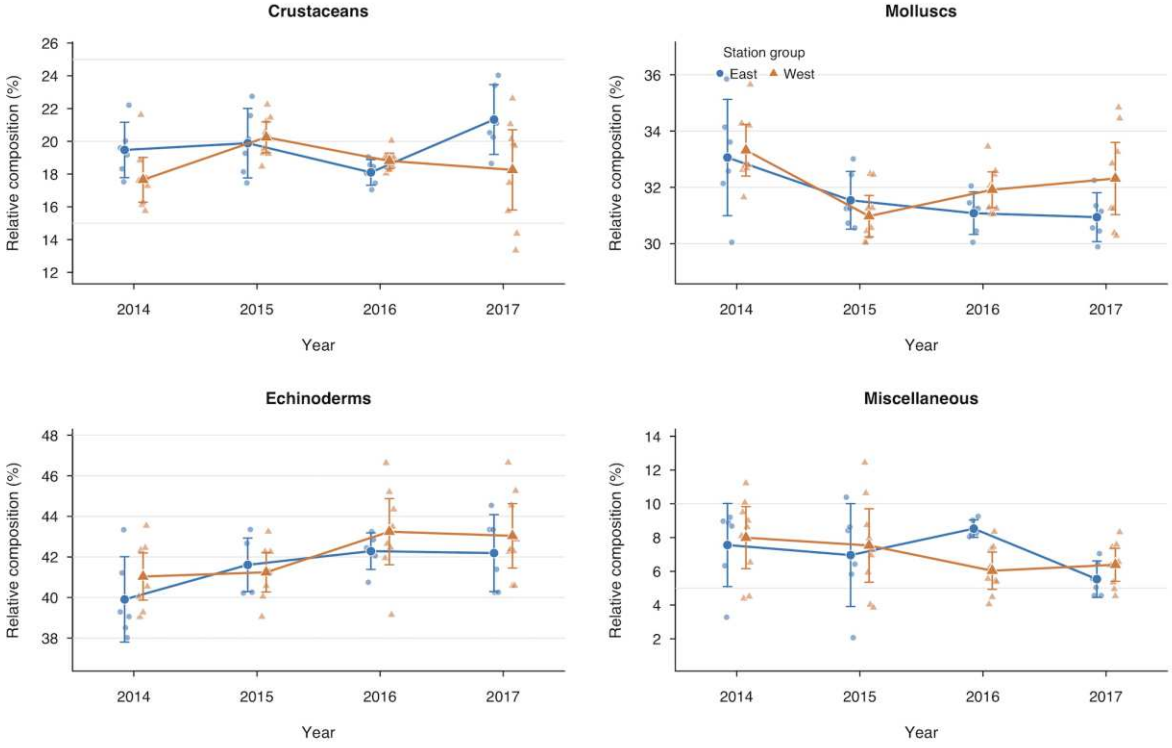


Fig. 9: Temporal variation in the relative composition (%) of major community groups (Crustaceans, Molluscs, Echinoderms, and Miscellaneous invertebrates) across eastern and western stations from 2014 to 2017. Points show individual station values; lines and error bars show regional means ± 95% confidence intervals.


Crustaceans
Molluscs
Echinoderms
Miscellaneous
Relative composition (%)
Year
2014
2015
2016
2017
Station group
East
West