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Revealing ENSO-Linked Oceanic and Atmospheric Controls Driving Coral Bleaching: Lessons from Sri Lanka's Fringing Reef Systems

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Abstract Font lettering Arial

Sri Lanka, a tropical island in the Indian Ocean, hosts a rich and highly biodiverse fringing coral reef system that has been increasingly degraded over the past few decades due to escalating anthropogenic pressures and recurrent ENSO-induced heatwaves. The physical mechanisms driving ENSO-related coral bleaching remain insufficiently understood, posing challenges to both local and global coral conservation efforts. This study aimed to address this knowledge gap by examining the influence of key physical drivers underlying coral bleaching across five reef sites in Sri Lanka during 1998, 2016, and 2024. The findings reveal that ENSO-linked sea surface temperature anomalies in the Indian Ocean, compounded by climate warming and radiative flux anomalies, intensified coral bleaching around Sri Lanka during these events. Though not fully explored, the positive feedback of delayed monsoon winds on shallow coral bleaching was evident in this study, mainly through triggering the latent heat flux anomaly. April was identified as the critical month for coral bleaching in Sri Lanka, as ENSO impacts peaked during April and extended into May. Furthermore, the study idealizes the occasional disparities of integrating global temperature data for predicting local-scale coral bleaching. These findings underscore the need for continuous *in situ* oceanic and atmospheric monitoring, long-term coral reef observation, and the integration of coral physiological responses into bleaching threshold assessments. Such approaches are essential not only for the Sri Lankan context but also globally, to enhance predictive capacity to safeguard these invaluable marine ecosystems from further degradation.

Key Words Tropical Indian Ocean, Sri Lanka, coral reef degradation, ENSO heat waves, coral conservation

Introduction

Coral reefs are well-known biodiversity hotspots, coastal ecosystem engineers, exquisite ecosystem services providers, and a major economic engine for many coastal communities. Coral reef ecosystem services range from food supply to tourism-based revenue for millions of coastal communities worldwide (Costanza et al. 2014). However, global coral reefs have been severely damaged over the past few decades with pollution (land-based and coastal), land-use changes, extreme marine heatwaves, and climate change. The decline of coral reefs is both ecologically and economically costly, impacting many low- to mid-income countries that heavily rely on coral ecosystem services (Hernández-Delgado 2015; Moberg and Folke 1999).

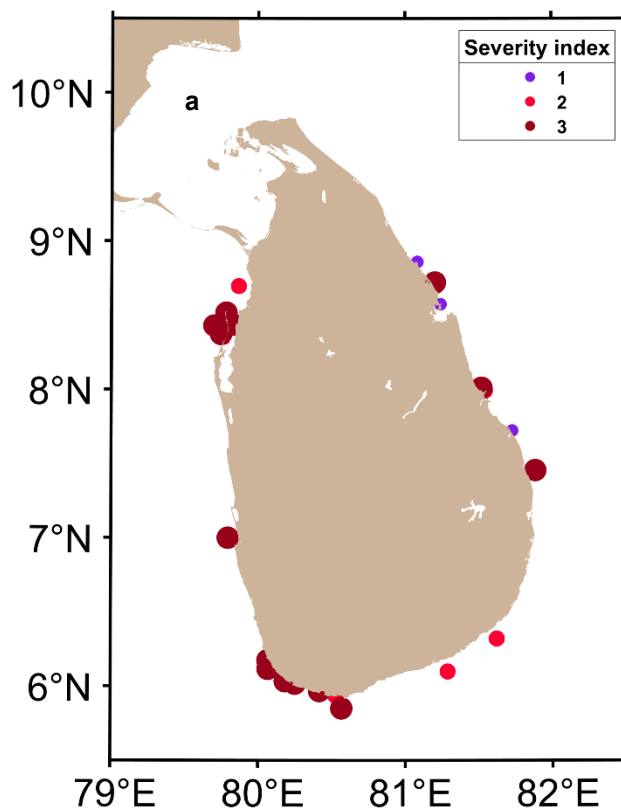
The thermal instability surges up with climatological (ocean warming) and periodic extreme heat events (i.e., El Niño Southern Oscillation-ENSO) are considered dominant, most extreme, and the most recent leading driver underlying worldwide coral bleaching and mortalities (Hughes et al. 2017; Obura et al. 2017). Heat stress builds up when the ambient water temperature exceeds the climatological maximum of summertime water temperatures over a prolonged period. (Brown et al. 2002; Glynn, 1996). The long-term accumulation of excess heat stress cascades physiological homeostasis between the coral host and the mutualistic endosymbiont algae (dinoflagellate algae in the genus *Symbiodinium*), triggering the coral host to expel the endosymbionts from its body tissues. The loss of endosymbionts leads to nutrient deprivation in the coral host, and vibrant coloration, which turns the coral tissues translucent and colorless, is called coral bleaching. Coral bleaching becomes irreversible and mortal with the extended thermal stress periods. The dominant role of climatic warming (Hoegh-Guldberg 2011; Hughes et al. 2017) and ENSO modulation (Cerutti et al. 2020; Dunne et al. 2020; Falco et al. 2020; Liu et al. 2022; McGowan and Theobald 2017) underlying the coral mass bleaching and mortality has been identified worldwide over the past decades.

Multiple physical mechanisms underpin global coral bleaching during ENSO events. The direct influence of Pacific Ocean sea surface temperature (SST) anomaly has been a primary driver of mass bleaching across numerous Pacific coral reefs, notably in 1998 and 2016 (Glynn et al. 2001; Kleypas et al. 2015). In contrast, SST anomalies transmitted through atmospheric teleconnections largely account for bleaching in reefs outside the Pacific (Goreau et al. 2000; Obura et al. 2017). Climate change further amplifies these ENSO-driven impacts by increasing the

severity, frequency, and duration of SST anomalies (Cai et al. 2014,2018). Beyond this, climatological SST rise imposes chronic thermal stress, raising the vulnerability of bleaching, population degradation, and extinction (Lough et al. 2018), as many coral reefs live close to their upper thermal limits (Berkelmans 2002). It is more pronounced in tropical coral reef systems, as tropical corals inhabit severely thermal-stressed environments, thus even modest temperature increases can trigger widespread bleaching (Hughes et al. 2017).

Coral reefs in the Tropical Indian Ocean (TIO) experienced severe bleaching during the extreme ENSO events of 1997–1998 and 2015–2016, coinciding with record-breaking SST anomalies (Linden et al. 2002; Obura et al. 2017). These anomalies were linked to Indo-Pacific inter-ocean basin interactions mediated by atmospheric teleconnections, which weakened and even reversed the Walker circulation over the TIO (Spencer et al. 2000; Yu and Rienecker, 1999). The circulation reversal generated a strongly positive SST anomaly in the western Indian Ocean, further intensified and displaced westward by anomalous easterly winds in the eastern basin (Webster et al., 1999; Yu and Rienecker 1999). As wind anomalies weakened during the early stages of the second El Niño year, this western Indian Ocean SST anomaly expanded across the basin, acting as the primary driver of mass bleaching in the TIO. In addition, anomalies in solar radiation, air temperature, cloud cover, wind speed, and air–sea fluxes, hallmarks of ENSO variability (Spencer et al. 2000; Yu and Rienecker 1999; Webster et al. 1999), exacerbated coral mortality through secondary positive feedback mechanisms.

Sri Lanka, a small tropical island in the Tropical Indian Ocean (TIO), hosts vibrant fringing reef systems along its continental shelf. These reefs, however, suffered extensive bleaching during the 1997–1998 and 2015–2016 ENSO events (Linden et al. 2002) (Fig. 1a), resulting in significant ecological and economic losses. Records from the 2024 ENSO event remain largely unavailable, aside from a few informal observations reported by nearby SCUBA divers (Fig. 1b)



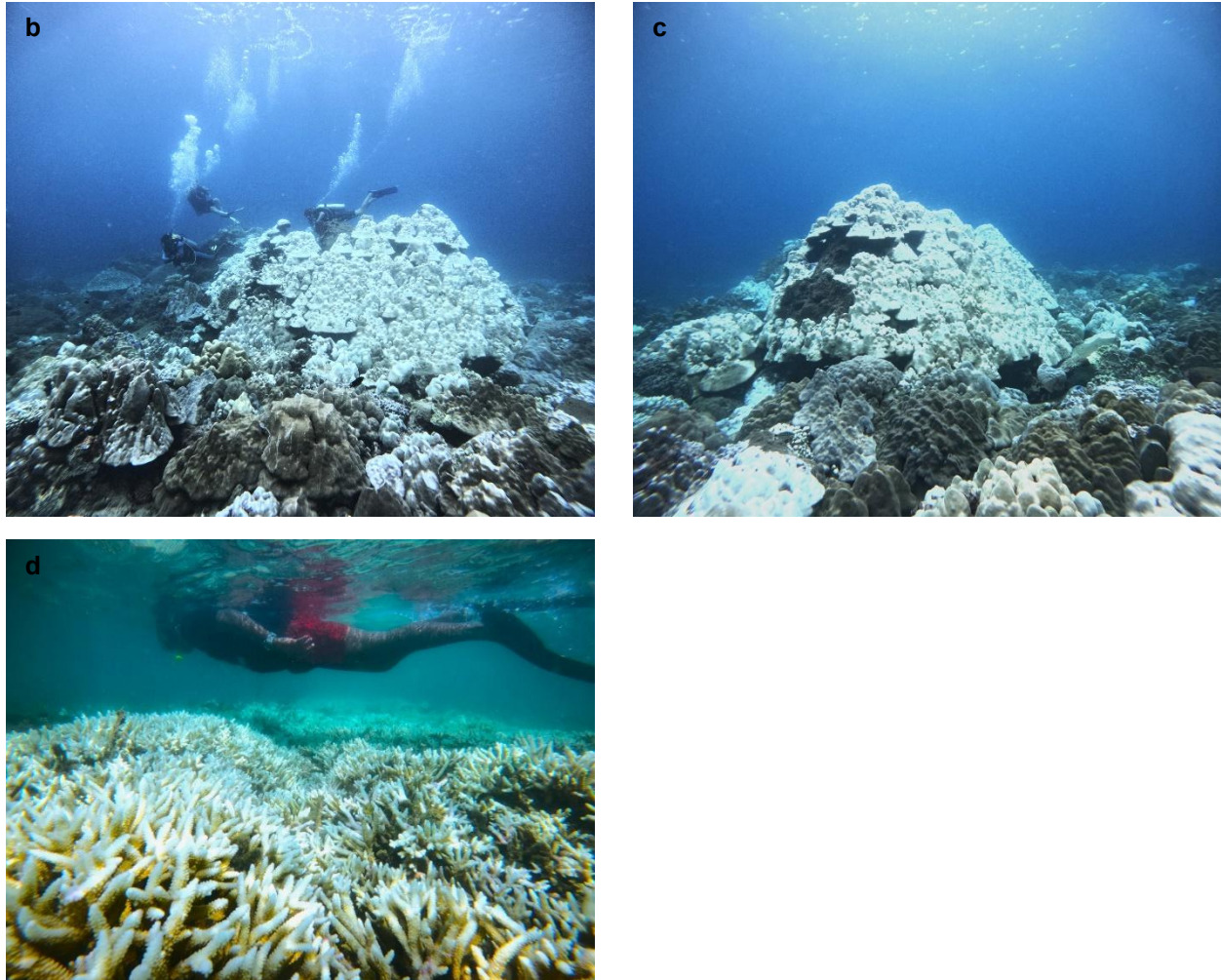


Fig. 1 Status of Coral bleaching in Sri Lanka during the major ENSO events. **a** Bleaching severity of corals around Sri Lanka past two decades. Data were extracted from Virgen-Urcelay and Donner 2023, **b-d** Visual observations of coral bleaching during the 2024 most recent ENSO event in Trincomalee and Kayankerni, East coast of Sri Lanka, **b** Coral bleaching at Dutch Bay, Trincomalee in 2024, **c** coral bleaching at Dutch Bay in 2025, **d** coral bleaching at Kayankerni shallow reef in 2025 (photos were captured by recreational SCUBA divers using GoPro Hero 8 camera)

A critical gap in Sri Lankan reef science is the limited assessment of the physiological and physical mechanisms driving bleaching during periods of thermal stress. Given the highly variable hydrodynamic conditions surrounding the island, it is reasonable to expect divergent coral responses to heat stress. Sri Lanka occupies a unique position between two marginal seas, the Arabian Sea and the Bay of Bengal, whose contrasting oceanographic characteristics shape local reef environments (Schott and McCreary 2001). The Bay of Bengal, bordering the east coast, is warmer and less saline, while the Arabian Sea, bordering the west coast, is cooler and more saline. Other coastal zones are influenced by seasonally reversing currents between these two basins. Human pressures further compound this variability; for example, reefs adjacent to the more polluted southwest–northwest coasts face higher anthropogenic stress compared to those along the east coast. These conditions position Sri Lanka as a unique natural laboratory for studying differential coral reef responses to both heat stress and anthropogenic impacts. Yet, significant data gaps hinder the full realization of this potential. The long-term fate of Sri Lankan reefs in the Anthropocene remains underexplored, and the absence of integrated, data-driven restoration strategies has led to fragmented conservation practices. This lack of scientific grounding not only threatens the sustainability of local reefs but also limits their contribution to broader global reef conservation efforts.

The overarching goal of this study is to address a critical knowledge gap by examining the mechanisms underlying coral bleaching in Sri Lankan reefs during the 1998, 2016, and 2024 ENSO warming events. Specifically, the study investigates the roles of recurring SST anomaly, long-term ocean warming, and local radiative budget anomaly (as a proxy for atmospheric forcing) in shaping the physical drivers of bleaching across these three major events. The analysis is based on freely accessible oceanographic and atmospheric datasets. The findings are intended to provide a foundational basis for future scientific assessments of coral reef responses.

Methods

Site selection

Five coral reef sites around the coast of Sri Lanka were selected for this analysis, representing the north, southwest, south, southeast, and east coasts, where a major portion of the fringing reef system extends around the country (Fig. 2). A $0.1^\circ \times 0.1^\circ$ grid box was demarcated on each site to extract reanalysis data in the downstream analysis with optimum spatial representation. Thondamanaru-TH (9.75-9.85N and 79.83-79.93E), Bar Reef marine sanctuary-BR (8.3-8.4N and 79.65-79.75E), Unawatuna- UN (5.92-6.02N and 80.22-80.32E), Kayankerni-KY (7.9-8N and 81.52-81.62E), and Pigeon Island-PI (8.65-8.75N and 81.17-81.27E) were picked as candidate sites for this analysis, representing the respective north, southwest, south, southeast, and east coasts.

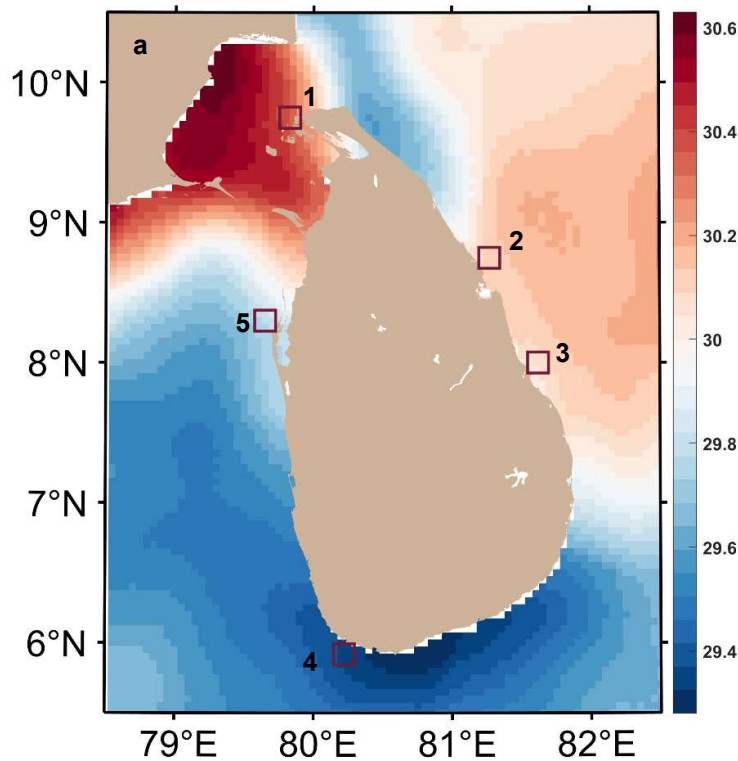


Fig. 2 Five selected coral reef sites around Sri Lanka. 1 -Thondamanaru (TH) from the northern coast, 2- Pigeon Island (PI) from the east coast, 3- Kayankerni (KY) from the east coast, 4- Unawatuna (UN) from the southern coast, and 5- Bar Reef (BR) from the northwestern coast. The locations are superimposed on the maximum monthly mean (MMM) sea surface temperature ($^{\circ}\text{C}$) distribution around Sri Lanka, derived from NOAA Coral Reef Watch data.

Satellite and reanalysis temperature data

The quantification of degrees of thermal stress posed on each coral reef site was a key focus of this study. For that, the 1-day 5km (0.05°) Sea Surface Temperature (SST) data products of the National Oceanic and Atmospheric Administration (NOAA) Coral Reef Watch (CRW) program (<https://coralreefwatch.noaa.gov/index.php>) were

retrieved in netCDF format covering the geographical domains of five selected coral reef sites for the three ENSO years 1998, 2016, and 2024. Downloaded night-time averaged SST and derived climatological maximum monthly mean (MMM) SST data were integrated to estimate the Degree of Heating Week (DHW) (Liu et al. 2017), as a proxy of heat stress accumulated in each site during the extreme heat events. The 0.1° grid box encompassed two 5km (0.05°) CRW pixel points; thus, two CRW SST time series and MMM values were extracted from each site, which were later averaged to get the site-wise mean SST time series and mean MMM. Estimated means were used to calculate the hotspot (the positive anomaly of temperature above the MMM) and the DHW, which is the cumulative hotspot values $\geq 1^{\circ}\text{C}$ per each grid box (a site) over 12 weeks (Liu et al. 2003, Skirving et al. 2006a) period. The $\text{DHW} \geq 4^{\circ}\text{C}$ was considered the coral bleaching critical threshold.

The atmospherically teleconnected SST anomaly in the Indian Ocean during ENSO years is widely recognized as a primary driver of coral bleaching. To quantify SST anomalies around Sri Lanka during the selected ENSO years, daily mean 5 km SST data were retrieved from the Marine Copernicus data server (<https://data.marine.copernicus.eu/products>). Two Global Ocean OSTIA Sea Surface Temperature and Sea Ice Reprocessed products (SST_GLO_SST_L4_REP_OBSERVATIONS_010_011 and 001, Worsfold et al. 2024) were combined to generate a composite daily SST time series spanning 1 January 1984 to 31 December 2024, covering the north Indian Ocean domain (0–15°N, 70–90°E) surrounding Sri Lanka. The daily SST values were then smoothed using a 7-day moving average filter and subsequently averaged to produce a monthly time series.

Radiative flux and surface wind data

Previous studies indicate that anomalous solar radiation can intensify oceanic thermal stress, particularly in shallow-water coral habitats during ENSO events (Zhang et al. 2013). To assess radiative flux anomalies around Sri Lanka during the three focal ENSO years, hourly reanalysis atmospheric data from the European Centre for Medium-Range Weather Forecasts (ERA5) were obtained via the Climate Data Store (<https://cds.climate.copernicus.eu/>) covering the Indian Ocean domain spanning 0–15°N and 70–90°E, encompassing Sri Lanka. Four mean surface flux components, net longwave radiation (msnlwrf), net shortwave radiation (msnswrf), latent heat flux (mslhf), and sensible heat flux (msshf), were extracted and combined following Equation 1 to calculate the net total solar radiation. Monthly mean radiative flux data were downloaded between 1984-1996 for the anomaly calculation and hourly radiative flux data were retrieved for the April-August period in each ENSO year.

$$Q_{\text{net}} = Q_{\text{swr}} + Q_{\text{lwr}} + Q_{\text{lt}} + Q_{\text{sh}} \text{ - Equation 1}$$

Where Q_{net} is the net total solar radiation flux, and the Q_{swr} is equivalent to ‘msnswrf’, Q_{lwr} is the ‘msnlwrf’, Q_{lt} is the ‘mslhf’, and Q_{sh} is the ‘msshf’. Hourly solar radiation data were averaged to generate the daily and monthly net solar radiation flux time series.

ERA5 hourly zonal and meridional wind at 10m (u_{10} and v_{10} respectively) were retrieved covering the Sri Lankan geographical domain of 0-10N and 79-82E for determining wind speed variability during the April-August season of three ENSO events. Respective monthly mean wind data were downloaded for the period between 1984-1996 for wind speed anomaly calculation. Wind speed was estimated following equation 2.

$$\text{Wind at 10m} = \sqrt{U_{10}^2 + V_{10}^2} \text{ - Equation 2}$$

Data analysis

An empirical orthogonal function (EOF) analysis was applied to identify the dominant modes of SST variability around Sri Lanka. Prior to the analysis, long-term climate trends and seasonal means were removed from the monthly mean SST anomaly time series. The EOF was performed for the spatial domain spanning 5.5–10°N and 79.5–82°E. The first principal component (PC1) was then compared against two oceanic indices, the Multivariate ENSO Index version 2 (MEI v2) and the Niño 3.4 index, both obtained from the NOAA Physical Sciences Laboratory (<https://psl.noaa.gov/data/timeseries/month/>). To assess the external forcing of SST variability, cross-correlations were computed between PC1 and each index using a lag interval of 10 months.

Monthly mean SST anomalies in the Indian Ocean basin surrounding Sri Lanka (April–August) for 1998, 2016, and 2024 were calculated by comparing the respective monthly mean SST values with the long-term climatology between 1984 and 1996. A similar approach was applied to estimate net solar radiation anomalies in the same domain, by contrasting monthly mean values of the three target ENSO years with the 1984–1996 climatological averages.

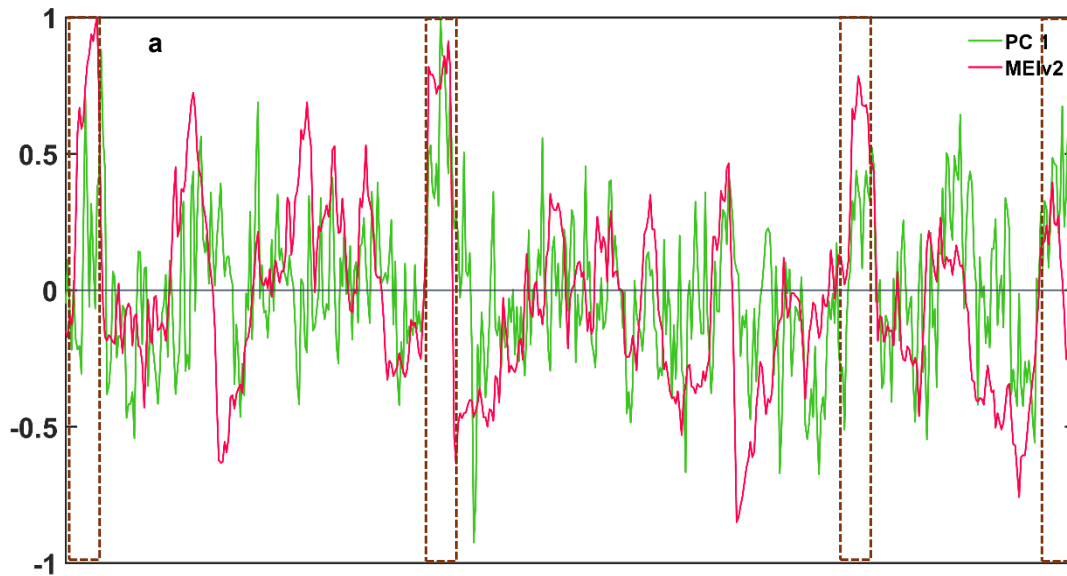
The influence of climate change on coral bleaching was assessed at three selected sites during the targeted ENSO years. Climate change impact was estimated as the deviation of monthly SST (April–August, 1984–2024) above the Maximum Monthly Mean (MMM) for each corresponding month at each site around Sri Lanka. Linear trends in these SST deviations were estimated using least-squares regression. All data analyses were performed in MATLAB (version 2022b), with the EOF analysis implemented using the ‘eof’ function in the Climate Data Toolbox for MATLAB (Greene et al. 2019).

Hourly solar radiation and the latent heat flux data were averaged for subsequent daily and monthly records first and subtracted from the long-term (1984–1996) average to estimate the anomalous solar radiation and latent heat flux of April to August months in three ENSO years. Three-day averaged wind speed data were calculated from ERA5 hourly data and subtracted from the long-term mean wind to get the 3-day averaged wind anomaly during the three April–August ENSO years.

Results

Dominant modes of Sea Surface Temperature variability

The EOF analysis revealed that the dominant mode, represented by the first principal component (PC1), explained 70.68% of the spatio-temporal SST variability between 1984 and 2024. PC1 exhibited four prominent peaks (green line in Fig. 3a, b) corresponding to the major ENSO years of 1982, 1998, 2016, and 2024 (dashed, dark-red rectangles in Fig. 3a, b). Comparison of standardized PC1 with standardized Niño 3.4 and MEI indices (red lines in Fig. 3a, b) indicated strong correspondence, with similar peaks in these years except for MEI in 2024. This alignment highlights the Pacific ENSO as the primary external driver of SST variability around Sri Lanka. Cross-correlation analysis (Fig. 3c) further revealed a phase lag between PC1 and the indices of approximately five months for Niño 3.4 and three months for MEI. The correlation was stronger with Niño 3.4 ($r^2 = -0.512$) than with MEI ($r^2 = -0.47$).



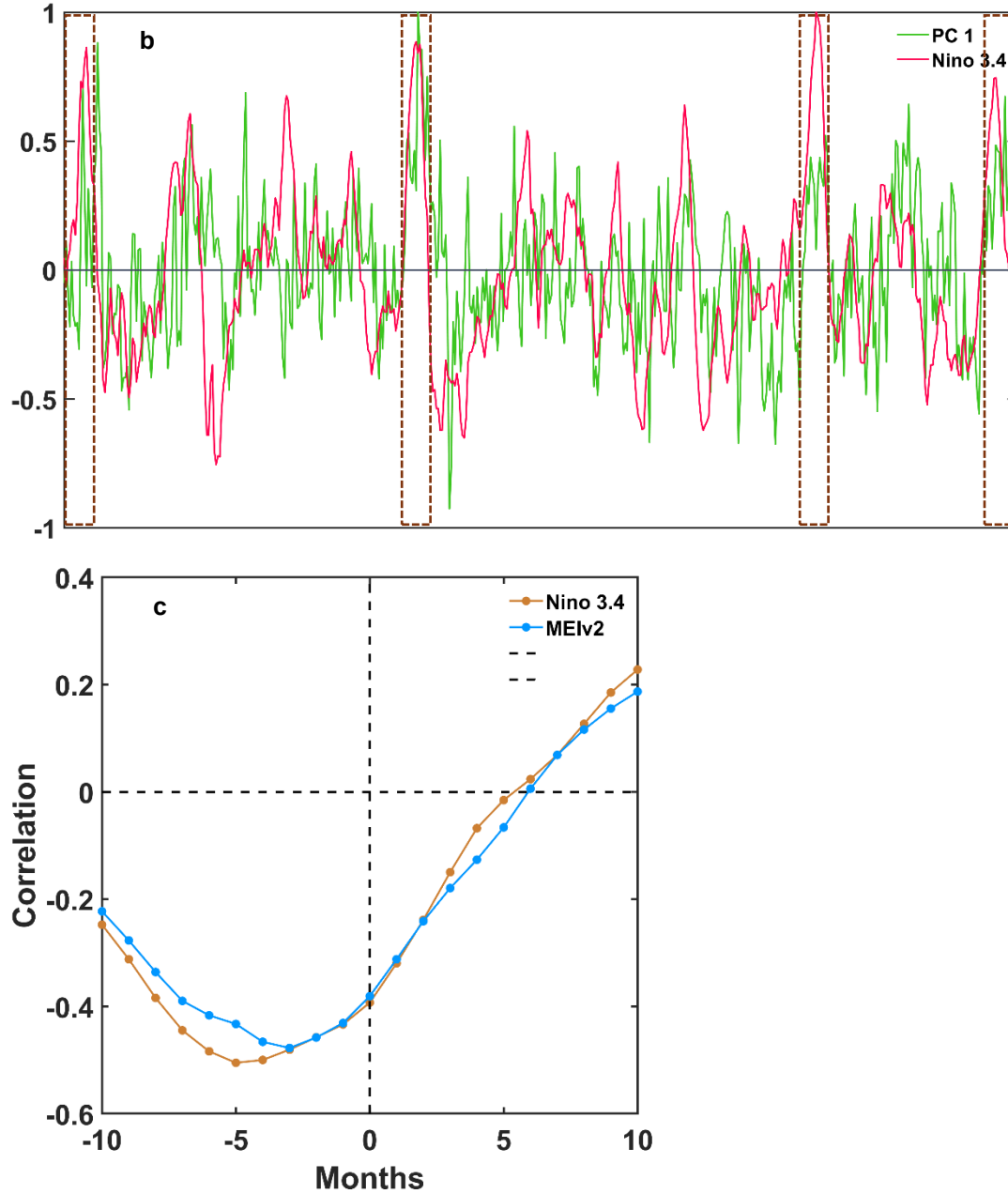


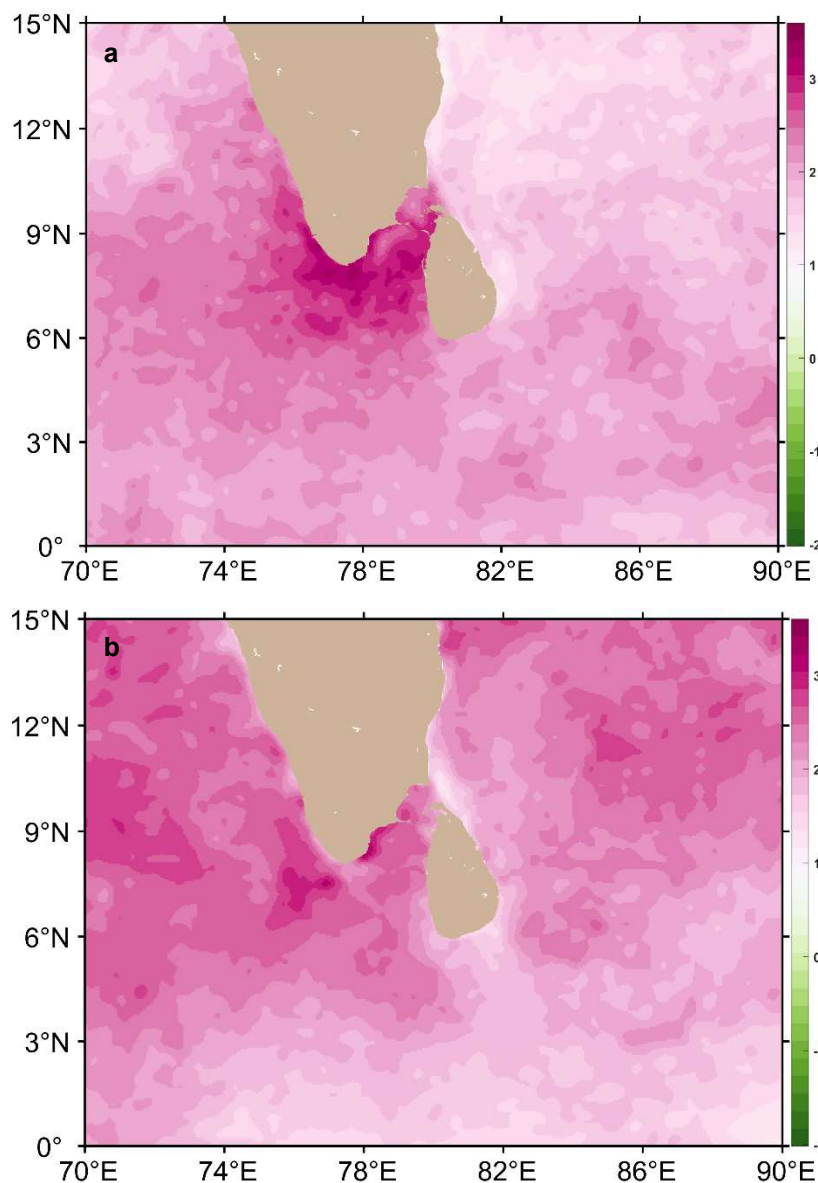
Fig. 3 The summary of the Empirical Orthogonal Function analysis of the sea surface temperature distribution around Sri Lanka (5.5–10°N and 79.5–82°E) during 1984–2024. **a** The comparison of the standardized first principal component of the EOF with the standardized Multivariate ENSO Index, **b** The comparison of the standardized first principal component of the EOF with the standardized Nino 3.4 Index, **c** The cross correlation between the first PC and the two indices in months. Grey shaded bars indicate the four major ENSO events in the Indian Ocean region (1982, 1998, 2016, and 2024)

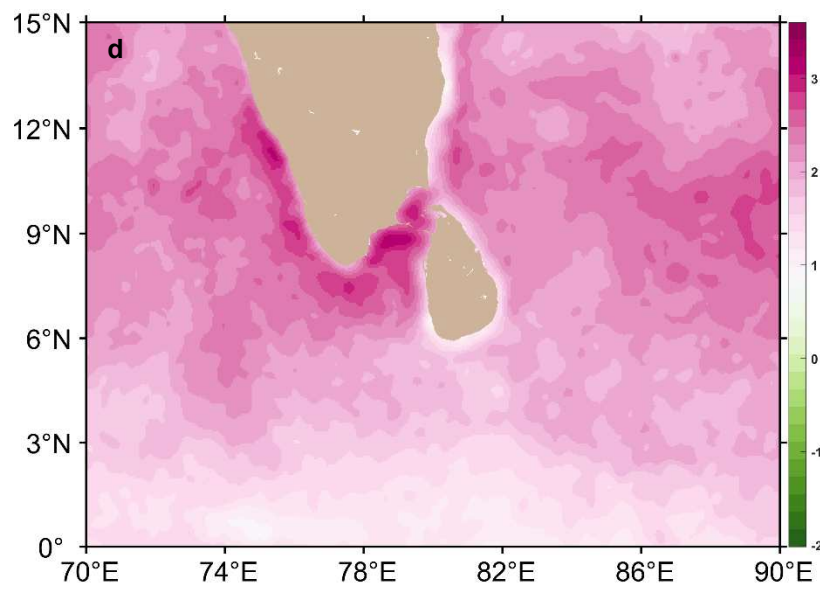
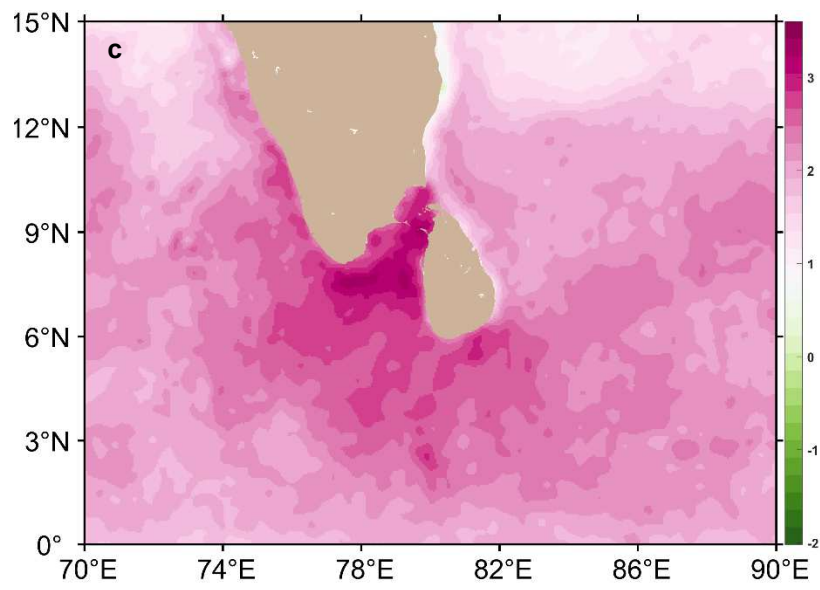
Sea Surface Temperature Anomaly around Sri Lanka

The surge of SST anomalies in the Tropical Indian Ocean (TIO), teleconnected to the Pacific ENSO through atmospheric circulation, is recognized as a major driver of coral bleaching in the region. To evaluate this effect around Sri Lanka, monthly mean SSTs during April–August of the three focal ENSO years were compared against the climatological mean for 1984–1996. The analysis revealed consistently strong and basin-wide positive SST

anomalies in April of all three ENSO years (Fig. 4a,c,e), with the most pronounced warming centered south of India and extending across the northern, western, and southern coasts of Sri Lanka. In addition, a clear longitudinal gradient emerged in April, with distinct differences in SST anomalies between the eastern and western margins of the island.

The basin-wide SST anomaly in May closely resembled the April pattern (Fig. 4b,d,f). However, the previously pronounced anomaly centered over southern India and Sri Lanka was less evident, while a weaker anomaly developed along Sri Lanka's continental shelf. During May, a distinct latitudinal gradient emerged across the surrounding Indian Ocean, with weaker anomalies near the equator transitioning to stronger positive values toward the north. In contrast, June marked the onset of a basin-wide transition from positive to negative anomalies (Fig. S1 in Supplement 1), which further intensified in July. Notably, a strong negative anomaly formed around the southern tip of India and the southern coast of Sri Lanka in June (Fig. S1a,c,e in Supplement 1) and expanded basin-wide by July (Fig. S1b,d,f in Supplement 1). A defining feature of this variability was the rapid shift from strong positive anomalies along Sri Lanka's northwest-to-southern coasts in April to pronounced negative anomalies by July.





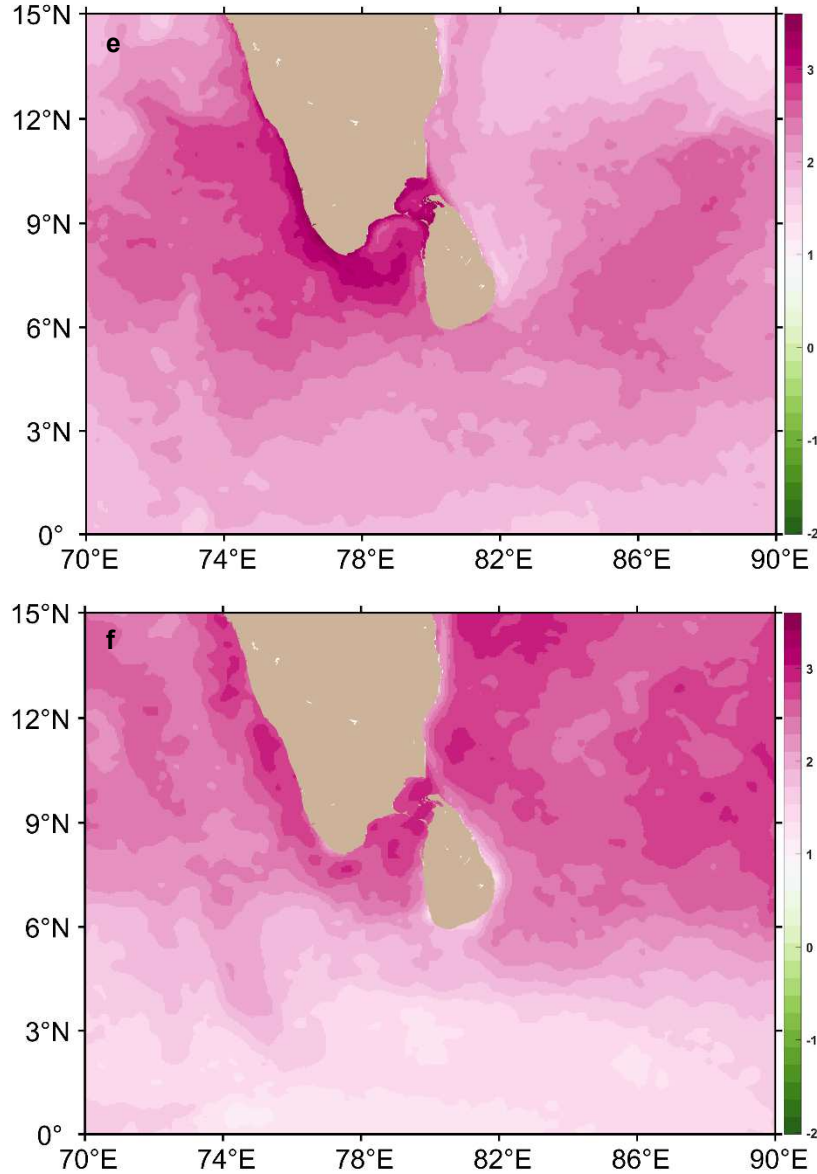


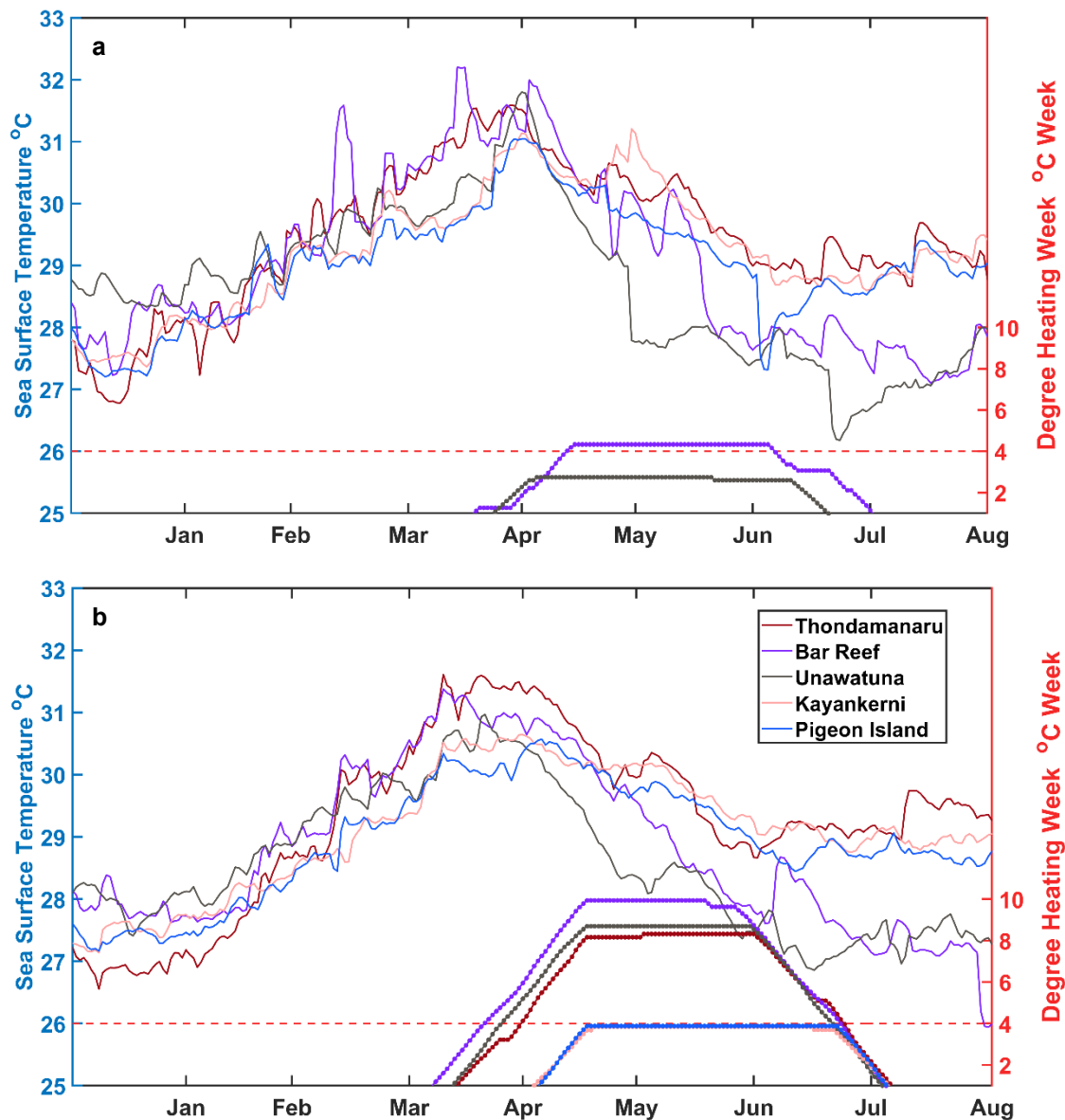
Fig. 4 Sea Surface Temperature (SST) anomaly in the Indian Ocean around Sri Lanka during April and May of 1998, 2016, and 2024 ENSO years. The anomaly is the difference between the respective monthly mean and the long-term (1984–1996) mean SST. **a,c, and e** SST anomaly of April in 1998, 2016, and 2024, **b,d, and f** SST anomaly of May in 1998, 2016, and 2024.

Sea Surface Temperature and thermal stress dynamics at survey sites

The sea surface temperature (SST) from January to August in 1998, 2016, and 2024 at each coral reef site exhibited a consistent pattern: a gradual increase beginning in mid-February, peaking in March–April, and then declining steadily from May onward (solid lines in Fig. 5). Across the three years, SST variability during this period ranged from 26 to 32°C at all sites. Heat stress accumulation, measured by degree heating weeks (DHW), began in mid-April at most sites in all three years, except at Kayankerni (KY) and Pigeon Island (PI), where it was delayed until early May in 2016 (Table 1). In 1998, Bar Reef (BR) on the northwestern coast experienced the highest thermal stress, with DHW exceeding 4°C for 54 days (May 13–July 5) (Fig. 5a). Unawatuna (UN) on the southern coast recorded the second-highest stress, with DHW approaching 3°C, while no other sites showed significant heat stress accumulation during the 1998 ENSO event.

Compared to 1998, heat stress was markedly higher across the five reef sites during the 2016 ENSO event. Bar Reef (BR) recorded the most extreme accumulation, with DHW peaking at 10°C between mid-May and late June. Thondamanaru (TH) and Unawatuna (UN) also experienced severe thermal stress, both exceeding 7°C from late May to early July, while Kayankerni (KY) and Pigeon Island (PI) reached nearly 4°C (Fig. 5b). The duration of bleaching-level heat stress (DHW $\geq 4^\circ\text{C}$) was the longest in 2016, persisting for 94 days at BR (April 19–July 23), 88 days at UN (April 24–July 21), 85 days at TH (April 28–July 23), and 66 days at both PI and KY (May 19–July 23). This represented a substantial increase compared to 1998, when BR recorded only 54 days of stress (May 13–July 5).

In contrast, the 2024 bleaching year showed less extreme heat accumulation than 2016 but still exceeded the critical DHW threshold. TH, BR, and UN recorded prolonged stress above 4°C for 83, 83, and 73 days, respectively, between April 27 and July 23 (Table 1, Fig. 5c). At both TH and BR, DHW reached 8°C, while at UN it stabilized at 6°C. Conversely, KY and PI on the eastern coast did not experience notable heat accumulation in 2024.



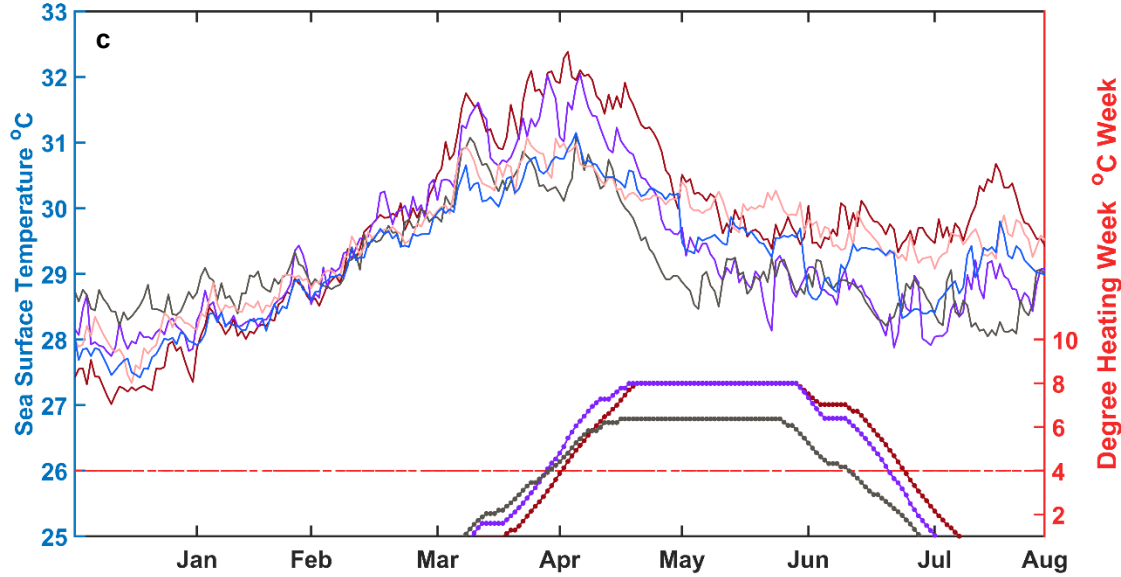


Fig. 5 Sea Surface Temperature and heat stress variability at five selected coral reef sites during three ENSO events 1998, 2016, and 2024. Solid lines indicate the SST variability and the dotted lines represent the heat stress accumulation as a proxy of degree of heating week (DHW). The red horizontal line indicates DHW=4°C, **a** SST and DHW variability during 1998, **b** SST and DHW variability during 2016, **c** SST and DHW variability during 2024

Climatological ocean warming at five coral reef sites

The deviation of the climatological monthly mean SST in April and May from their respective maximum monthly mean (MMM) values at the five selected sites showed clear upward trends (Table 1, Fig. 6). The grid-averaged April mean SST (1982–2024) exhibited the largest deviation from MMM in 1998, followed by subsequent peak years (Fig. 6a). Among the sites, Bar Reef (BR) consistently recorded the highest positive anomalies, while Pigeon Island (PI) exhibited the lowest troughs. The rate of increase in April SST deviation was fastest at Thondamanaru (TH- 0.24°C year⁻¹) and slowest at Kayankerni (KY- 0.13°C year⁻¹) (Table 1). Notably, in four sites (all except PI), the SST–MMM deviation was second-highest in 2024 (after 1998), highlighting a potential intensification of warming in recent years.

A similar rising trend was observed for May SST deviations between 1984 and 2024 (Fig. 6b). In May 1998, BR and Unawatuna (UN) registered the second-highest peaks, while TH and PI showed the deepest troughs in May 1999, contrasting with the April time series. The fastest rate of increase in May was recorded at BR (0.15°C year⁻¹), whereas PI had the slowest trend (0.08°C year⁻¹) (Table 1). A key feature of the May time series was the record-high peaks in 2024 at TH and BR, which were nearly 0.5°C above the 1998 peaks, underscoring a potential amplification of ocean warming at these sites in the most recent period. By contrast, neither June nor July exhibited a consistent up- or downward trend across ENSO years (data not shown). Variability during these months was largely random, with no discernible site-specific patterns.

Table 1. Annual rising rates of the deviation of grid-averaged SST from maximum monthly means of April and May between 1984–2024 to five selected sites

	April		May	
	Annual rate	MMM	Annual rate	MMM
Thondamanaru TH	0.24	30.21	0.18	30
Bar Reef BR	0.19	29.86	0.19	29.6
Unawatuna UN	0.23	29.34	0.15	28.95
Kayankerni KY	0.13	30.04	0.13	30.04
Pigeon Island PI	0.2	29.51	0.08	30.09

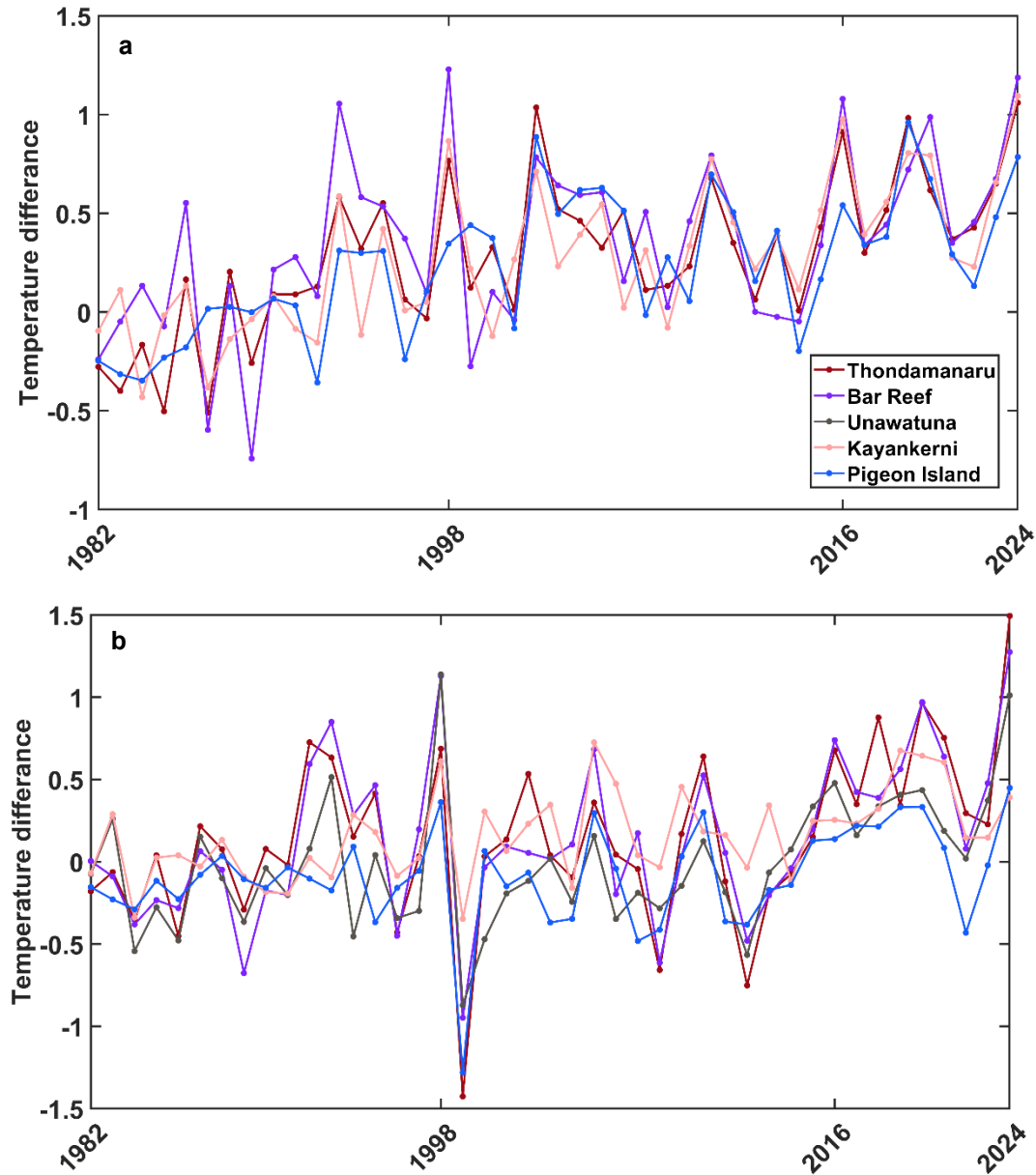
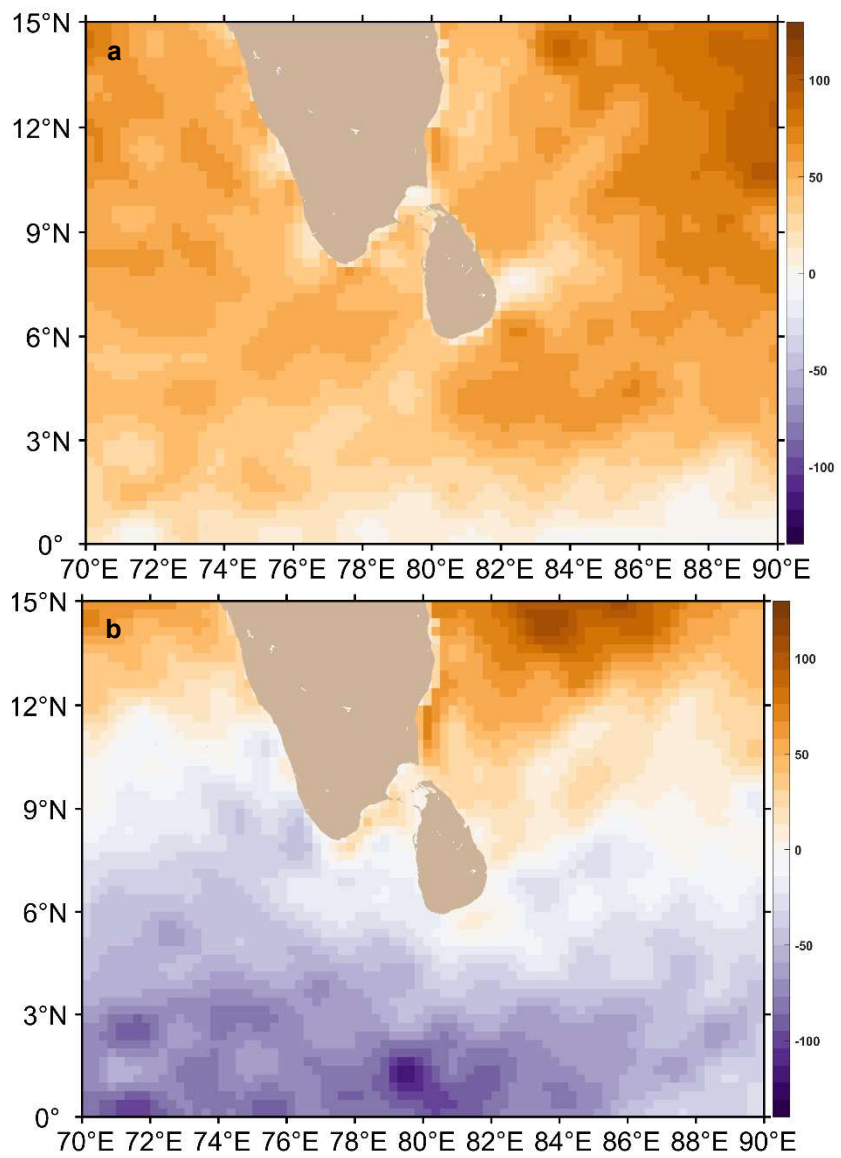
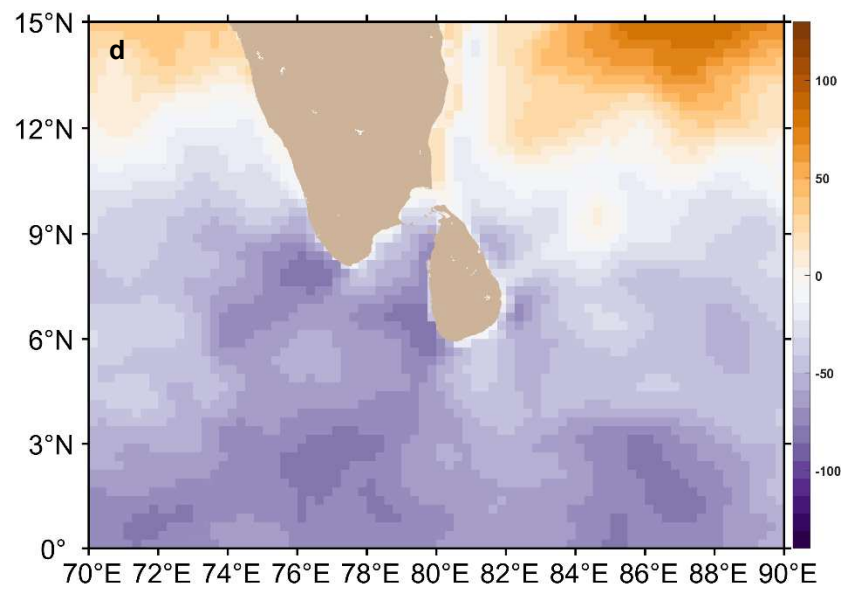
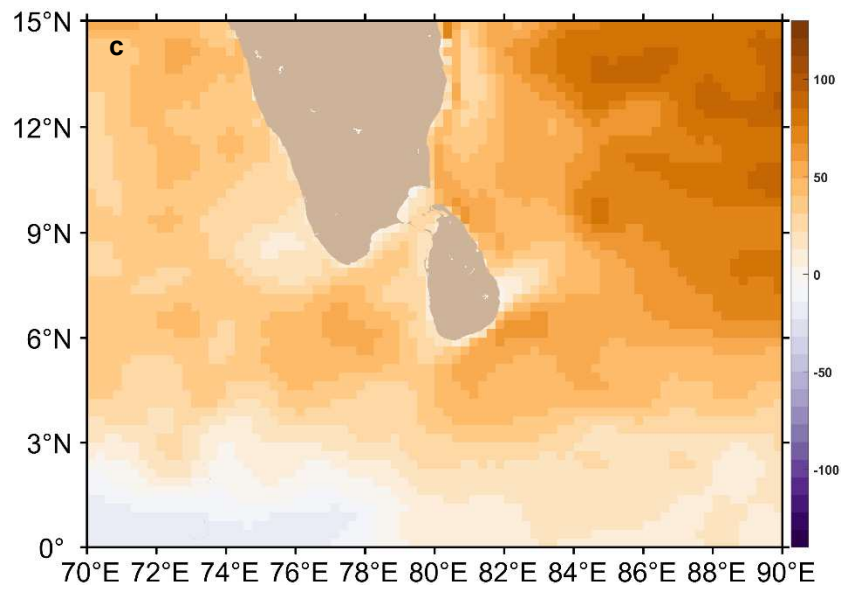


Fig. 6 Climatological rise of the deviation of monthly mean sea surface temperature from its climatological maximum monthly mean during April and May between 1982-2024 period at five study sites, **a** the rise of deviation in April, **b** the rise of deviation in May

The radiative budget and wind anomaly around Sri Lanka during ENSO years

April of 1998, 2016, and 2024 were marked by basin-wide positive net solar radiation anomalies (Fig. 7a, c, e). The strongest anomalies were centered over the Sri Lankan domain in April but transitioned to negative values by May in each ENSO year (Fig. 7b, d, f). The May anomalies displayed a pronounced latitudinal gradient, with negative values confined to the 0–12°N band and positive anomalies dominating higher latitudes. These localized negative anomalies in May subsequently intensified and expanded to a basin-wide scale, persisting through June and July (data not shown).





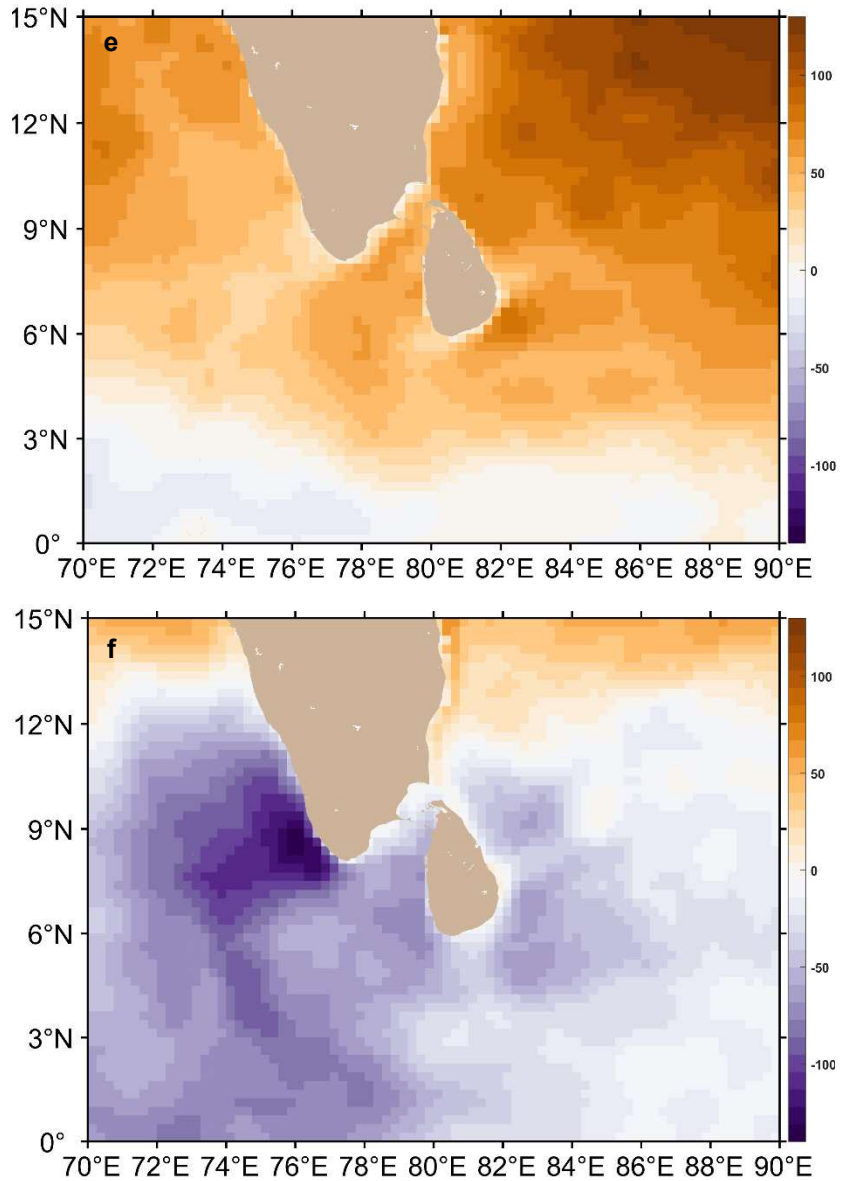


Fig. 7 The anomalous solar radiation in April and May during the three ENSO years around Sri Lanka. The anomaly is the difference between the respective monthly mean, and the long term (1984-1996) mean solar radiation, **a,c,e** Solar radiation anomaly during April of 1998,2016, and 2024 respectively, **b,d,f** Solar radiation anomaly during May of 1998,2016, and 2024 respectively.

The latent heat flux anomaly, an indicator of surface heat loss through evaporation, exhibited notable spatial variations during April across all three ENSO years (Fig. S2a,c,e in Supplement 1). Overall, positive anomalies were observed over the ocean surrounding Sri Lanka, indicating heat gain at the sea surface, while negative anomalies representing heat loss were detected along the coastal regions, including the five surveyed sites (Fig. S2a,c,e in Supplement 1). In contrast, the anomaly remained positive along the coastal zone during the first two weeks of May (01–20 May) in all three ENSO years, signifying a prolonged accumulation of heat energy at the ocean surface (Fig. S2b,f in Supplement 1). The following months, June, July, and August, displayed a general trend of negative latent heat flux anomalies (data not shown).

Furthermore, the 3-day averaged ERA5 wind speed anomaly revealed a delayed onset of the southwest monsoon winds around Sri Lanka, shifting from the typical onset period in the second week of May (IMD) to the latter half of May during all three ENSO years (Fig. S3 in Supplement 1).

Discussion

In this study, we focused on determining potential physical underpinnings of coral bleaching around Sri Lanka during three recent ENSO years. An exquisite fringing coral reef inhabited the shallow, continental shelf around the country, which underwent rapid degradation in recent decades. The remaining reefs are more likely to be considered ‘Anthropocene reefs’, as they have been surviving under severe anthropogenic pressure exerted from multiple sources, i.e., ocean warming, intermittent extreme heat events, pollution, fisheries, and physical human disturbances. Therefore, the potential of Sri Lankan reefs to serve as a natural laboratory for characterizing the physiological and molecular mechanisms of tropical coral reefs underlying the evolution to the Anthropocene is very high, making them remarkable in both local and global coral conservation and restoration agendas. However, Sri Lankan coral reef research remains largely confined to post-bleaching status records, apart from two studies by Arulanathan et al. 2021 and Thilakarathne et al. 2023 that addressed molecular and physical mechanisms. This study aimed to close this critical data gap by evaluating the key physical underpinnings of coral bleaching in Sri Lanka during three recent ENSO events, which could serve as a foundation for identifying reef sites with better thermal tolerances and for decision-making in coral reef management and conservation activities.

Five coral reef sites were picked for this analysis, representing the entire coastal zone of Sri Lanka. The thermal distribution of each coral reef site is unique, shaped by the spatial and temporal variability of hydrodynamics around the island, as the East Coast, which faces the relatively warmer Bay of Bengal, is warmer than the West Coast that faces the cooler Arabian Sea (Schott and McCreary 2001). Besides, the shallow and highly stratified waters of the Palk Bay (Azeez et al. 2016) have the potential to make the northern coastal region of Sri Lanka the warmest, resulting in the highest mean annual temperatures along the island’s north coast (Fig. 2). A clear spatial heterogeneity of the maximum monthly mean (MMM) distribution supports to ground this fact, that the TH (north coast) recorded the highest MMM, PI and KY (east coast) recorded the next warmest MMM, and the BR and UN (northwestern and south coasts) recorded the lowest MMM among the sampling sites (Fig. 2). Considering this contrasting thermal distribution, it is reasonable to posit differential adaptation mechanisms, and acclimatization potentials in coral conspecifics inhabiting the thermal gradients, supported by the inherent variabilities in coral genomic landscape, holobiont, and the coral microbiome. Differential acclimatization potentials (Palumbi et al. 2014), standing genetic variations (Dixon et al. 2015), and the symbiont shuffling mechanism (Cunning et al. 2015) provide solid explanations for how coral conspecifics maintain optimum physiological homeostasis at different thermal regimes. Coral conspecifics inhabiting the contrasting thermal environments around Sri Lanka may similarly regulate endosymbiont composition to maintain the optimum thermal tolerance. In other words, for example, *A. hyacinths* at TH may contain a higher concentration of Symbiodinium D, compared to *A. hyacinths* at UN, with more Symbiodinium clade B, in the corresponding ambient temperature variability. Going further deep, the spatially varying acclimatization, genetic, and also microbiome composition diversity could help Sri Lankan coral conspecifics to thrive in varying thermal regimes around Sri Lanka, but no records are available. Therefore, the drawing of scientifically robust physiological and molecular-mechanical-based conclusions remains rather speculative. Besides, multiple anthropogenic stressors, such as pollution, human disturbances, and surface runoffs, have actively been suppressing the coral reefs inhabiting around Sri Lanka; thus, the coral reef endosymbiont relationships, genetic, and microbiome diversities could be more complicated than expected. To that end, properly planned common ground experiments should be conducted to untangle the complex molecular and physiological mechanism networks underlying coral reef responses to anthropogenic stressors in Sri Lanka.

The EOF analysis clearly captured the four extreme SST events around Sri Lanka in 1982, 1998, 2016, and 2024. These four years are dominant ENSO years; thus, the notion that the SST variability around Sri Lanka was primarily modulated by the Pacific ENSO was promising. The first principal component (PC1), or the dominant mode, accounted for 70.68% (green line in Fig. 3) of the SST variability, compared to the second PC (variance = 10.62%). The SST peaks of the first PC in 1982, 1998, and 2024 were well distinct, compared to 2016, which showed a relatively weaker jump. 2016 was an Indian Ocean Dipole (IOD) negative year (Lu et al. 2018), therefore, the

likelihood of shared influence of both modes in the SST variability in 2016 was high, resulting in a weak peak observed in the first PC of the EOF analysis. The dominant first PC correlated with the two ENSO indices with a phase lag (5 months in the Nina 3.4 and 3 months in the MEI) (Fig. 3c), indicating the delayed response of the local SST variability to the Pacific ENSO. Yu and Rienecker 1999 demonstrated that the phase lag between the onset of the Indian Ocean SST anomaly and the Pacific ENSO, that the SST anomaly in the Indian Ocean was triggered in March-May 1998, long after the Pacific ENSO SST anomaly in 1997. The same situation is expected in other ENSO events, where the SST variability around Sri Lanka was triggered with a phase lag, particularly during the second year of the Pacific ENSO events of 1997-1998, 2015-2106, and 2023-2024.

The positive influence of the Indian Ocean SST anomaly as a frontline physical driver of coral bleaching around Sri Lanka was evident here. The SST anomaly analysis clearly demonstrated the spread of basin-wide SST anomaly during April of each ENSO year (Fig. 4a), which is a known Indian Oceanic response to Pacific ENSO. The reversal of the atmospheric Walker circulation in the Indian Ocean, together with wind anomalies, triggered an SST anomaly that was initially confined to the western IO basin during the early phase of ENSO (western ocean warm pool), before gradually propagating basin-wide as the wind anomalies weakened in the later phase (Yu and Rienecker 1999). As ENSO progressed, the equatorial SST anomaly propagated poleward and impacted Sri Lanka, exhibiting an asymmetric distribution with the strongest positive anomalies along the western periphery (southwest, west, northwest, and north coasts), while only weak positive anomalies along the eastern margin during April (Fig. 4a,c,e). This asymmetry accounted for the spatial heterogeneity in heat stress accumulation, which commenced in mid-April across most survey sites. The peak form of the April positive SST anomaly persisted throughout May (Fig. 4b,d, and f) in each year and gradually transitioned into a basin-wide negative anomaly in consecutive June and July months in each ENSO year (Fig. S1 in Supplement 1).

The Degree Heating Week (DHW) analysis yielded key insights into the differential patterns of heat stress accumulation across the five coral reef sites. Heat stress accumulated in coral reef sites with the onset of the SST anomaly around Sri Lanka. BR, at the northwestern coast, that exhibited the largest divergence between the SST anomaly and the MMM, recorded the greatest heat accumulation, in other words the highest degree heating weeks (DHW), in consecutive three ENSO events (4, 10, and 8 °C·DHW in 1998, 2016, and 2024, respectively) (Fig. 5). Analogous SST anomalies were evident at the TH and UN sites, which corresponded to the subsequent highest levels of heat accumulation across the three ENSO years (Fig. 5). Visual observations of mass coral bleaching at the BR were reported in the post bleaching period of 1998 and 2016 (Linden et al. 2002; Virgen-Urcelay and Donner 2023), that supported the summary of DHW analysis. However, the absence of visual observations of coral bleaching at BR in 2024 renders the validation of the DHW-based conclusion incomplete. The coral bleaching status in TH during any of the three ENSO years was not reported due to the three-decade-long civil war in the northern part of Sri Lanka. Arunlananthan et al. 2021 reported the existence of coral rubble in the TH site and suggested that these rubbles could be remnants of past coral bleaching events. Contrastingly, heat stress accumulation was not observed in the DHW analysis for the two East Coast sites, KY, and PI, in 1998 and 2024 (DHW=0°C), but only in 2016 (DHW ~4°C) (Fig. 5). This lower heat stress accumulation could be linked to the relatively weaker difference between April and May SST anomaly (Fig.4) and the relatively higher MMM (Fig.2). The conclusion of the DHW analysis, a minimal coral bleaching in PI during 1998, was supported by the visual observations, as reported in Linden et al. 2002. No proper bleaching assessment data are available to support the coral bleaching in PI during the 2024 event, but SCUBA divers reported severe coral bleaching in 2024 and 2025 at Dutch Bay (Fig. 1b), a site very close to PI, suggesting a strong likelihood of bleaching in PI, which was inconsistent with the DHW-based assessment. KY is among the most pristine and biodiverse coral reef systems in Sri Lanka, with no prior records of bleaching during the three ENSO events. Nonetheless, visual observations in 2025 (Fig. 1b) confirmed bleaching at the site, indicating that bleaching likely occurred during the 2024 ENSO as well, despite the absence of direct records.

The inconsistencies between DHW-derived records and site-specific bleaching assessments, particularly at PI and KY, highlight a critical consideration that the global-scale observation frameworks, such as NOAA CRW's DHW, may not reliably capture local-scale coral bleaching vulnerabilities. Local-scale coral bleaching is linked to extreme diurnal SST variabilities driven by flux anomalies (Zhang et al. 2013), species-specific local adaptations, acclimatization potential, and site-specific coral species composition. This inconsistency should be recognized as a

significant limitation of predicting local-scale coral bleaching from global-scale remotely sensed SST data. Such circumstances could hinder the achievement of the expected outcome, which is conserving coral reefs during periods of thermal stress. Proper assessments of site-specific coral species composition, inherent thermal tolerance, and species-level physiological and molecular adaptive or acclimatization mechanisms are essential to inform more effective conservation strategies during ENSO events. Accurate *in situ* SST and radiative flux measurements are key to developing the accurate bleaching prediction systems; thus, the capacity building on SST ground monitoring and implementation of physiology and molecular-oriented predicting endpoints, such as the eDHW (Leggat et al. 2022), should be critically integrated in future coral bleaching predictions in vulnerable coral reef sites, including sensitive locations like PI and KY.

The effect of climate change on coral bleaching was quantified as the proxy difference between April–May monthly SSTs and the MMM for 1982–2024. This difference exhibited an upward linear trend at all sites, indicating a progressive rise in SST–MMM deviations over 43 years (Fig. 5, Table 1). The deviations were particularly pronounced during April of the three ENSO years, underscoring ENSO’s influence on local SST variability during the late phase of the first inter-monsoon. A site-specific deviation between the SST and MMM wasn’t clearly observed, but more often BR site deviation was at the top edge, while the PI site recorded the lowest deviation. The trend of the May deviation was pronounced as in April, but only two significant peaks emerged (Fig. 5b). A key outcome of this analysis is the persistent rise in April–May SST divergence, which translates to escalating thermal stress at each coral site. Such unprecedented stress pushes corals toward their upper thermal tolerance limits, reducing the safe margin for survival during abrupt extreme heatwaves (e.g., ENSO events), unless thermal plasticity or adaptive mechanisms significantly enhance tolerance (Hackerott et al. 2021; Matz et al. 2018). Tropical coral conspecifics inhabit regions with ambient environmental temperature close to their maximum thermal tolerance compared to their sub-tropical or polar conspecifics. Therefore, the continuously rising ocean temperature is likely to keep tropical coral reefs under constant thermal pressure, leading to an increase in their acute bleaching vulnerability during ENSO events. In other words, as shown in this study, Sri Lanka’s coral reefs are highly threatened by climatic ocean warming, as SSTs are rapidly surpassing historical climatological thermal levels. Nonetheless, site-specific coral adaptive capacity, physiological backups (e.g., endosymbiont shuffling), and coral microbiome dynamics may provide some resilience. However, rigorous empirical validation is necessary to substantiate this potential beyond speculation.

In the final stage of this study, we assessed the influence of solar radiation anomalies on coral bleaching during the three ENSO years. Similar to the SST anomaly pattern, a pronounced basin-wide positive anomaly occurred in April of each year (Fig. 6a), increasing bleaching vulnerability, particularly at shallow reef crests, during the early phase of the Indian Ocean ENSO. Many reefs in PI, KY, and the shoreline break of TH occur in water shallower than 2 m, making them highly susceptible to extreme solar radiation. The cloudless skies typical of ENSO years, linked to the reversal of the Indian Ocean Walker circulation (Yu and Rienecker 1999) exposed the sea surface directly to intense solar radiation, driving rapid daytime warming in the upper ocean. This process likely contributed to bleaching at shallow reefs in Sri Lanka, such as PI and KY, where DHW estimates did not fully explain bleaching events in 1998 and 2024. However, this hypothesis requires empirical validation through *in situ* monitoring of solar radiation and SST, particularly at radiation-sensitive reefs like PI and KY.

The anomaly peaked in April, turned negative in May (Fig. 6b), and remained so into June and beyond (data not shown). The onset of the southwest monsoon in May, characterized by heavy rainfall and overcast skies, reduced surface radiation and created negative anomalies in our analysis. Such conditions may provide a short-lived refuge for shallow reefs to recover, although the simultaneous rise in SST could offset this benefit. We emphasize that bleaching driven by solar radiation anomalies in remote, shallow reefs may not be adequately captured in global, daily-averaged remotely sensed SST records; thus, the strengthening of ground-based monitoring systems should be critically considered to improve the predictability of shallow reef bleaching during ENSO events.

The delayed onset of the southwest monsoon wind is a salient feature of ENSO events, known to exert a positive feedback effect on coral bleaching in the Indian Ocean (Liu et al. 2022). In this study, a late onset of the southwest monsoon wind was observed over the Sri Lankan region during all three ENSO years (Fig. S3 in Supplement 1). Although its direct influence on coral bleaching was not extensively characterized here, positive feedback of delayed

monsoon to depreciate the surface heat loss through evaporation was evident in the study, which reflected as a positive latent heat flux anomaly during the first two weeks of May in each ENSO year (Fig. S2b,d,f in Supplement 1). This positive anomaly, indicative of heat retention at the ocean surface, is dynamically linked to weakened evaporative cooling under reduced wind speeds. Further analyses are required to comprehensively characterize the interactions between monsoon dynamics and coral bleaching, particularly in relation to other basin-scale oceanic processes such as the Indian Ocean Dipole (IOD).

Conclusions

In summary, this analysis identified the positive feedback of SST anomalies, long-term climate warming, and the radiative flux anomalies linked to the delayed onset of monsoon winds jointly modulated coral bleaching around Sri Lanka. Heat stress, expressed as degree heating weeks (DHW), reached the critical 4 °C threshold in mid-to-late April during all three ENSO events, persisted through May, and declined between June and August. April emerged as the most critical month for bleaching, when SST anomalies, background warming, and solar radiation anomalies acted synergistically to intensify thermal stress. In May, the influence of SST anomalies, climate warming, and the positive latent heat flux anomaly persisted, while solar radiation anomalies diminished gradually with the onset of the southwest monsoon. Bleaching susceptibility varied markedly among reef sites. BR exhibited the greatest vulnerability due to its wide deviation between SST anomalies and the MMM, whereas reefs along the east coast were relatively protected by narrower deviations. Notably, mismatches between DHW-based predictions and in situ bleaching observations highlight the urgent need for improved ground-based monitoring of SST and radiative flux to enhance predictive accuracy. Furthermore, advancing knowledge of the thermal tolerance, acclimatization, and adaptive capacity of Sri Lankan corals remains critical for developing robust resilience strategies.

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Author Contribution

AH conceptualized the paper, analyzed data, compiled, and edited the document.

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Data availability

All the data utilized for this study are freely accessible to anyone interested.

Declarations

Conflict of interest

The author confirms that there is no conflict of interest in this paper

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