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REVISITING THE CORAL REEFS OF THE ANDAMAN SEA – FACTORS AFFECTING RESILIENCE, RECOVERY AND REEF REFUGIA

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Abstract Although coral reefs of the Andaman Sea have in recent decades been subject to global factors known to impact the extent of live coral cover, such as increasing sea temperatures, short-term extreme temperature events and rising sea levels, nonetheless unlike many other reefs worldwide, there has not been any steady decline in cover. Indeed, over the last decade, the trajectory at sites which have been monitored is one of a pronounced recovery in live coral cover following an extreme widespread temperature-induced bleaching in 2010, restoring many cover values back to the early 1990s when records commenced. While susceptible to extreme bleaching events, Andaman Sea corals have been shown to display some resilience to rising sea temperatures, particularly those

living in habitats subject to physical extremes such as highly fluctuating sea temperatures, inshore turbidity and aerial exposure. Such locations have been described as potential refugia where corals are adapted to cope with these physical stresses that in turn ameliorate the effects of elevated sea temperatures. Future climate scenarios and other anthropogenic influences will undoubtedly challenge these reefs with potential increasing frequency and intensity of El Niño Southern Oscillation and positive Indian Ocean Dipole events, modification of internal wave regimes and rising sea levels. A better understanding of the scope of corals to respond to a warming climate is dependent on closer collaboration of countries surrounding the Andaman Sea in research areas such as coral reef monitoring, coral growth and reproduction studies and interdisciplinary studies to establish patterns of larval dispersal that would identify sources and sinks of juvenile corals.

Keywords: Andaman Sea; Coral Reefs; Resilience; El Niño Southern Oscillation; Indian Ocean Dipole; Large Amplitude Internal Waves; Sea Surface Temperature; Refugia; Climate Change

Introduction

Despite advances in recent years, the coral reefs of the Andaman Sea in the eastern Indian Ocean remain one of the least studied reef systems in the tropics (Brown 2007). In the latest global coral reef assessments (Souter et al. 2020a, Kimura et al. 2022, Chan et al. 2023), they stand out as being among one of the few areas in the world where the coral reef status appears not to be in decline. Recent publications have also highlighted areas in the Andaman Sea, which appear less vulnerable to climate change (Hoegh-Guldberg et al. 2018) or experience resilience to bleaching events because of mitigating physical factors (Wall et al. 2015, Sully et al. 2019, Sully & van Woesik 2020, Bachman et al. 2022). In this review, we examine these assessments together with the most detailed and up-to-date surveys that have been undertaken in the region and discuss factors that might be responsible for any recovery and resilience at sites within the region.

In an earlier review, Brown (2007) documented the characteristics of the Andaman Sea and its coral reefs. In the intervening years, there has been increased interest in understanding the complex oceanography of the region (Chatterjee et al. 2017, Liu et al. 2018, Magalhaes & da Silva 2018, Mohanty et al. 2018, Raju et al. 2020, Sun et al. 2021, Yang et al. 2021a,b, Yadidya & Rao 2022). Recent studies have also described the short- and longer-term effects of tectonic activity following the 2004 and 2005 Sumatran earthquakes (Meltzner et al. 2006, Satirapod et al. 2013, Simons et al. 2019, Naeije et al. 2022) and the incidence and frequency of major ocean/atmosphere phenomena such as El Niño Southern Oscillation (ENSO) and the Indian Ocean Dipole (IOD) (Abram et al. 2008, Aparna et al. 2012, Cai et al. 2014, 2018, Doi et al. 2020, Lu & Ren 2020). All these factors have potentially significant influence on the coral reefs of the Andaman Sea such as the effects of large amplitude internal waves (LAIWs) on coral thermal resilience and physiology (Roder et al. 2010, Wall et al. 2015, Schmidt et al. 2016), the impact of uplift and subsidence of reef areas through land movement (Satirapod et al. 2013, Simons et al. 2019, Naeije et al. 2022) and exposure to extreme seawater temperatures (Phongsuwan & Chansang 2012) and fluctuating sea levels associated with ENSO and IOD climate phenomena (Brown et al. 2019, Dunne et al. 2021).

Coupled with these research developments, there have also been increased efforts to monitor the reef status in countries such as Myanmar, India (Andaman and Nicobar Islands) and Indonesia (Aceh Province), which have provided a much more comprehensive overview of reef condition in the Andaman Sea than has been available hitherto (Guest et al. 2012, Souter et al. 2020a, Kimura et al. 2022). In the Thai-Andaman Sea (this term referring to the Thai sea area within the Andaman Sea), long-term monitoring records currently span over 43 years for selected intertidal reefs and over 33 years for specific subtidal reefs, offering the ability to track reef responses to a variety of environmental disturbances alongside reef recovery times and coral community changes (Phongsuwan & Chansang 2012, Brown et al. 2019, Dunne et al. 2021). Similar long-term monitoring data is

available in the Acehese-Andaman Sea from 2003 (Baird et al. 2005, Campbell et al. 2012), while less extensive records exist for the Andaman Islands and Myanmar (this paper).

This review will also explore factors that have affected the coral reefs in the region over the last 16 years and assess the extent to which reef sites in the Andaman Sea might act as thermal refugia in an era of rapid climate change, before highlighting research areas worthy of attention in future work.

Regional background

The Andaman Sea is a semi-enclosed marginal sea in the northeast tropical Indian Ocean (Figure 1). It is surrounded by four countries with India (Andaman and Nicobar Islands) and Indonesia (Aceh Province, Sumatra) on its western border, and Myanmar and Thailand to the east on the Thai/Malay peninsula. This marginal sea is connected to the Bay of Bengal to the north and east through shallow passages (100–200 m deep), which include the Preparis Channel north of the Andaman Islands, the Ten Degree Channel between the Andaman and Nicobar Islands and The Great Channel between the Nicobar Islands and the northern tip of Sumatra. Details of the geological history of the region, the complex sea floor topography, and major physical factors affecting the coral reefs were provided in Brown (2007) together with descriptions of the fringing reef types found along coastlines and around offshore islands.

One coastline that has received recent attention is that of Myanmar for which little information was available 16 years ago (Tun 2013, Holmes et al. 2014, Howard et al. 2014, Obura et al. 2014, Howard 2018, Lunn et al. 2022). Here fringing coral reefs are distributed along the Rakhine coast north of the Ayeyarwady (Irrawaddy) delta, around the Coco islands south of the delta and in the Myeik Archipelago along the southern mainland coast of Myanmar (Lunn et al. 2022). The reefs of the Rakhine coast are less well developed than those in the Myeik Archipelago, with the southernmost structures described as rocky outcrops with low coral cover (Murray-Jones et al. 2016). Inshore areas are extremely turbid because of river discharges, and coral reef growth is limited by high sedimentation, seasonal storms and strong wave action (Murray-Jones et al. 2016). On the Rakhine coasts, inshore coral diversity is low, with the reefs being dominated by *Porites* and *Acropora* species. Inner reefs in the Myeik Archipelago further south also receive river discharge, but water quality improves around offshore islands (Lunn et al. 2022). On the inner reefs of the Myeik Archipelago, *Acropora* species dominate, while the outer fringing reefs are dominated by *Porites* species (Howard 2018). A total of 287 coral species were recorded throughout the Myeik Archipelago in a survey carried out in 2014 by Obura et al. (2014), a figure comparable with that noted further south in the Thai-Andaman Sea where approximately 270 species of hard corals have been recorded with the most abundant species, in terms of areal cover, being *Porites lutea*, *Porites rus*, *Acropora muricata*, *Acropora intermedia* and *Prevotella nigrescens* (Phongsuwan & Chansang 1992).

Climate-related variables and ocean/atmosphere phenomena and their influence on coral reefs in the Andaman Sea

Sea surface temperature

To illustrate the sea temperature regime in the Andaman Sea, monthly mean sea surface temperatures (MMSST) for 5 km grid squares at locations selected because of the availability of recent coral reef monitoring information have been calculated for the period 1985–2022 using NOAA Coral Watch Data (https://pae-paha.pacioos.hawaii.edu/erddap/griddap/dhw_5km.html) (see Supplementary Information) (Table 1).

While these monthly mean values imply a relatively warm and stable temperature regime throughout the year within a narrow temperature range, in fact corals at many sites within the Andaman Sea are now known to experience significant sea surface temperature (SST) fluctuations

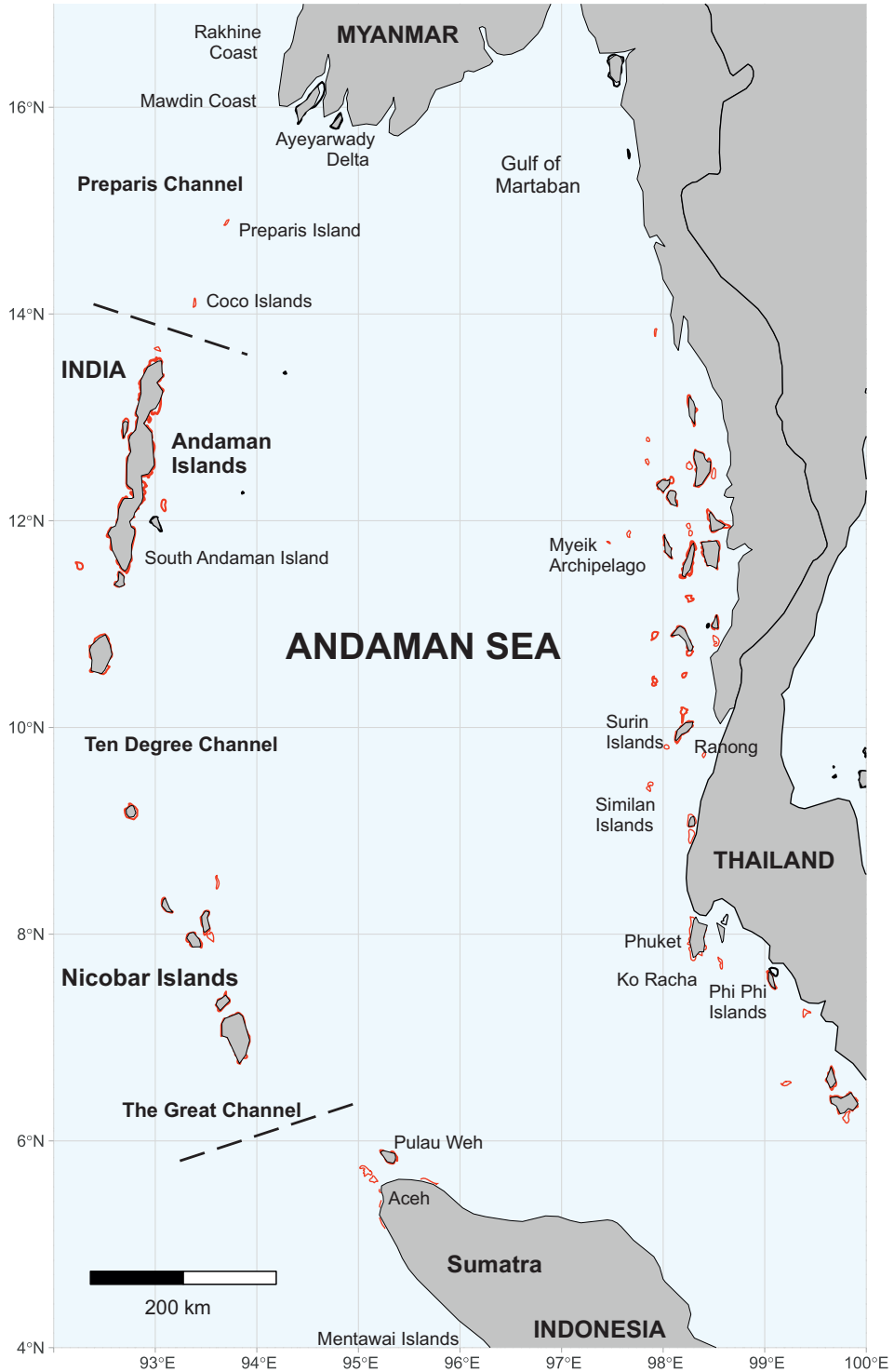


Figure 1 Map of the Andaman Sea showing approximate distribution of fringing reefs (coloured red) along shorelines.

Table 1 Annual Minimum and Maximum Monthly Mean Sea Surface Temperatures (°C) (1985–2002) in the Andaman Sea and the Month of Occurrence

| Month of occurrence | Minimum | Maximum | |
|----------------------|---------|---------|-------|
| | January | April | May |
| SITE | | | |
| Phuket | 28.4 | | 30.2 |
| Surin | 28.2 | 29.92 | |
| Myeik Archipelago | 27.8 | | 29.77 |
| South Andaman Island | 27.8 | 30.2 | |
| Pulau Weh, Aceh | 28.5 | 29.67 | |

within short 24-hour periods. For example, reefs on the western sides of the Similan Islands in the Thai-Andaman Sea experience an annual MMSST of 28.5°C with a range of 5.2°C, but subtidal corals are also subject to rapid daily temperature depressions of ~10°C through the influence of internal waves on seawater mixing. These rapid SST fluctuations occur throughout the year on the west sides of the Similan Islands but are particularly marked during the northeast monsoon season (November–April) when seasonal SSTs are maximal (Schmidt & Richter 2013). Similar, but smaller, effects have also been noted on reefs on the east side of the Surin Islands further north on the Thai-Andaman Sea coast, where corals on the reef slope were subject to 4°C depressions during strong upwelling in April–May (Figure 2). Intertidal coral reefs, which are widespread on coasts surrounding the Andaman Sea (Brown 2007), are also subject to wide temperature fluctuations within a 24-hour period due to spring tide aerial exposure in the dry northeast monsoon season (November–May) when tidal ranges can exceed 3 m (Brown 2007). For example, measurements of temperature in coral calices on intertidal coral surfaces at this time show daily ranges of up to 13.75°C (maximum 39.48°C, minimum 25.73°C), compared to daily ranges of 3.13°C during subsequent neap tides (Sweet et al. 2017).

The long-term temporal rise in bulk sea temperatures in the region continues to the present day, with values previously reported at Phuket in the Thai-Andaman Sea (Brown 2007) between 1946 and 1995 (45 years) at 0.126°C per decade (Brown et al. 1996), between 1980 and 2010 (30 years) at 0.142°C per decade (Tanzil et al. 2013), between 1979 and 2017 at 0.159°C per decade (38 years) (Brown et al. 2019) and most recently 1985–2022 at 0.204°C per decade (Figure 3). These rates are mirrored by a similar value from Pulau Weh in north Sumatra, where an increase of 0.161°C per decade was recorded over a 59-year period (1951–2010) (Guest et al. 2012). Since the rate of temperature rise is dependent on the database and time interval chosen and in order to obtain a comparative estimate for all the sites of interest, a 35-year period was selected (1985–2022) using NOAA Coral Watch Data (see Supplementary Information). This analysis gave increases of 0.204°C, 0.202°C and 0.201°C per decade for Phuket, Surin Islands and South Andaman, respectively, and 0.172°C per decade in both the Myeik Archipelago and Pulau Weh. Although the rise appears similar at the former three sites and slightly lower for the Myeik Archipelago and Pulau Weh, the overlap of confidence limits in the data meant that there was no significant difference among all sites (see Supplementary Information). Although such rates compare with similar rates of warming on Caribbean reefs (Bove et al. 2022), in the Andaman Sea, corals are living much closer to their lethal temperatures than their Caribbean counterparts (Brown et al. 1996), and for reefs around Phuket, SST has risen by ~0.8°C in the last 38 years (1985–2023).

Rates of sea temperature warming appear to be higher for locations in the Andaman Sea compared with those for Singapore or sites on the east side of the Thai-Malay peninsula (Tanzil et al. 2013). Indeed, since the 1950s, it appears that the tropical Indian Ocean has warmed faster than

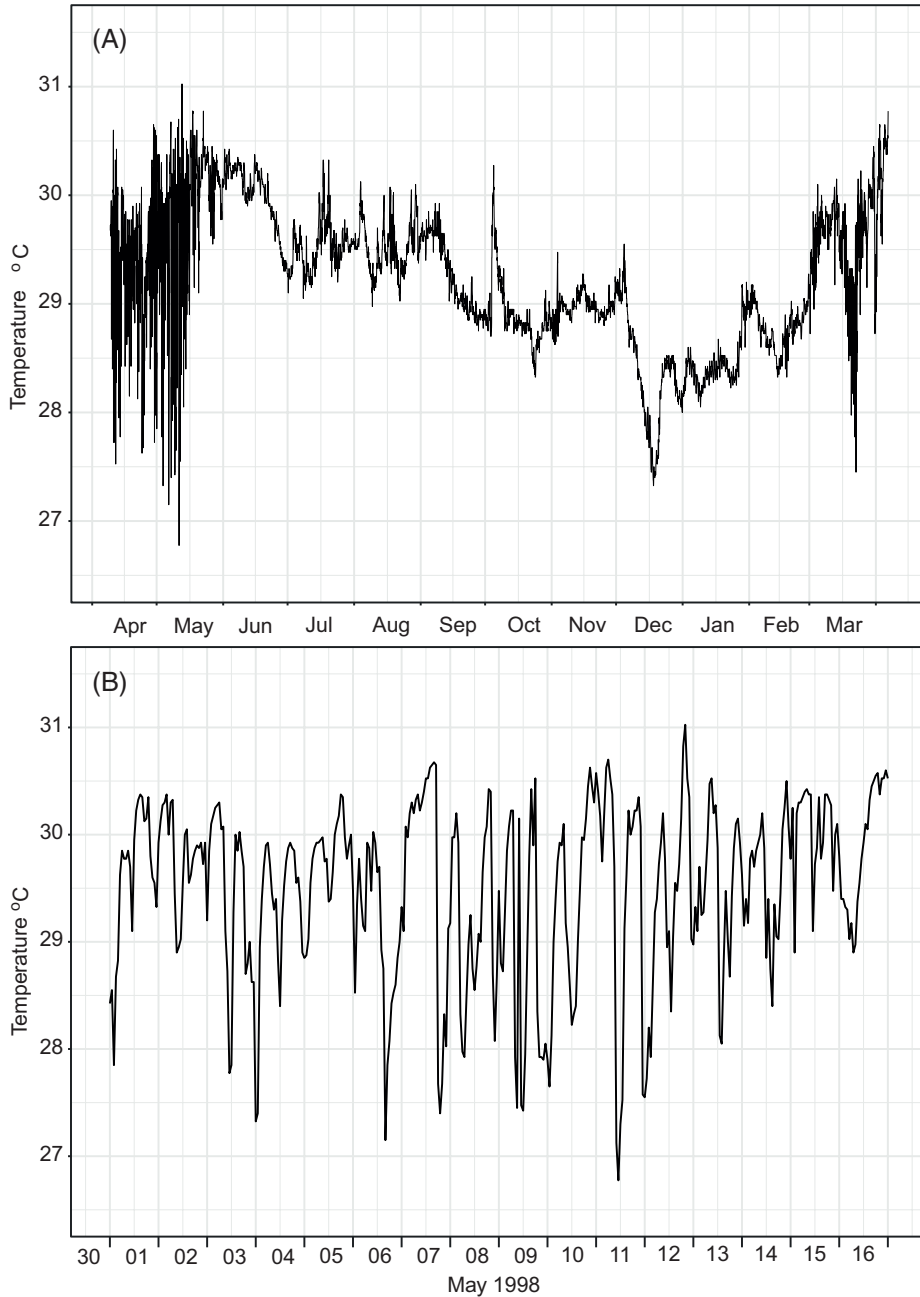


Figure 2 Hourly sea temperature plots for Ao Mayai, Surin Nuea, in the Surin Islands, Thailand, at 10m depth. (A) April 1998–March 1999. (B) 1–16 May 1998.

other tropical ocean basins (Han et al. 2014), and it has been shown that the advection of heat transported by strengthening westerly winds to the western equatorial Indian Ocean, which in turn is transported zonally eastward, has played a significant role in this basin-wide warming in recent decades (Mohan et al. 2021). The mechanism potentially involved is complex and involves

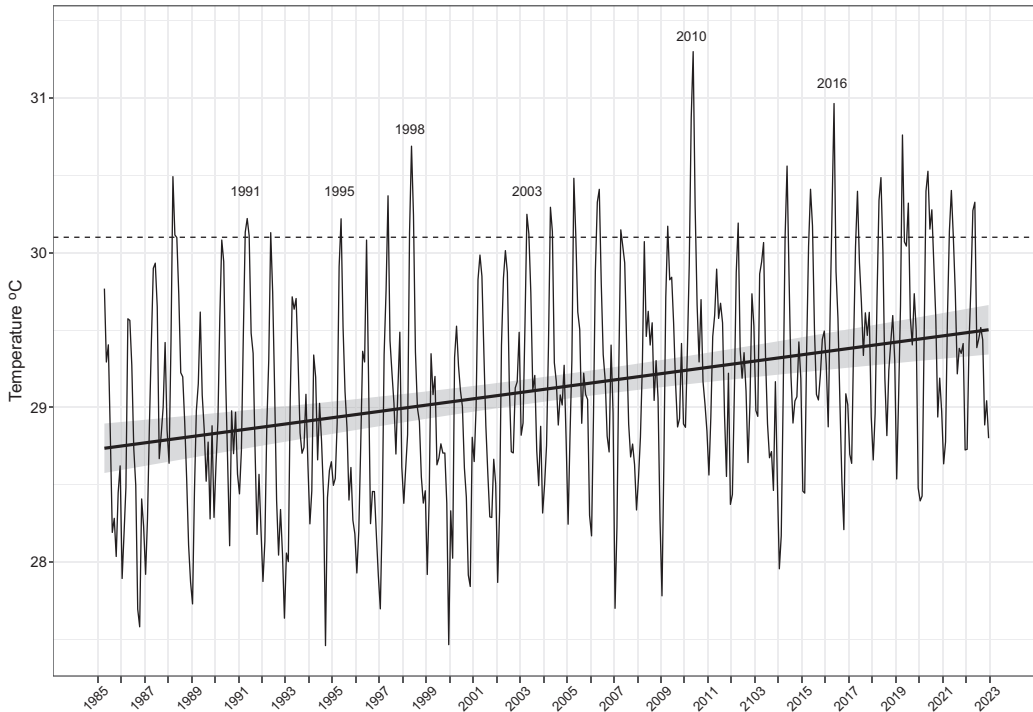


Figure 3 Monthly mean sea surface temperature (MMSST) 1985–2022 for the Phuket region. (Data from NOAA CoralTemp Version 1.0, 5 km grid centred on 7.825°N 98.275°E: https://pae-paha.pacioos.hawaii.edu/erddap/griddap/dhw_5km.html). Dashed line represents putative coral bleaching threshold of 30.1°C (established after the first bleaching episode in 1991 and which may have altered in subsequent years), with labels identifying years when significant bleaching was recorded (after Brown et al. 2019). Solid line represents the linear trend (Generalised Additive Mixed Model AR3) over time, 0.204°C per decade with 95% confidence intervals (grey shading).

the Walker circulation, an equatorial zonal atmospheric convection over the Indo-Pacific warm pool. The lower branch of the Walker circulation is associated with westerlies in the Indian Ocean, which are important in driving decadal variations in the Indian Ocean, though there is yet no scientific consensus on whether the circulation is weakening or strengthening to influence the observed strengthened westerly winds (Han et al. 2014).

At Phuket, there have been a number of years where SSTs exceeded a putative coral bleaching threshold (Brown et al. 1996) when extensive thermally induced coral bleaching was recorded (1991, 1995, 1998, 2003, 2010 and 2016) (Figure 3). These bleaching events (up to 2010) also occurred throughout the Thai-Andaman Sea. All, apart from an extreme event in 2010, were assessed as mild to moderate (Phongsuwan & Chansang 2012). In contrast, in 2010, coral mortality on subtidal reefs around Phuket and the offshore Phi Phi islands was in the range of 44%–99% (Phongsuwan & Chansang 2012), while the shallowest intertidal reefs suffered 40% mortality and took ~8 years to recover (Brown et al. 2019). Extensive coral bleaching was again noted in 2016 at both intertidal and subtidal sites in the Thai-Andaman Sea, but the effects on coral reefs were minimal as temperatures then fell with the arrival of the cloudy and wet south-west monsoon (Brown et al. 2019, Yeemin & Sutthacheep 2022), and many branching species showed a diminished bleaching response (Putchim et al. 2017). A very mild and short-lived bleaching also occurred in 2019 when 10%–30% of corals paleed at sites surrounding Phuket but rapidly recovered with the onset of the wet monsoon

(L. Putchim – personal communication). While it is possible that corals are becoming more thermally tolerant to seasonal peaks in SST (Maynard et al. 2008, Sully et al. 2019, Hughes et al. 2021, Lachs et al. 2023), which induce milder bleaching events than those noted at the same or lower temperatures in the early 1990s, in the Andaman Sea, many other factors such as prior experience of high solar radiation before the seasonal maximum SST, upwelling of cool water and time of monsoon onset complicate such an assessment (Dunne & Brown 2001, Phongsuwan & Chansang 2012).

In the Andaman Islands, temperature-induced coral bleaching was reported in 1998, 2002, 2005, 2010 and 2016, though this was assessed as mild and patchy in 2002 and 2005 (Majumdar et al. 2018). Again, the 2010 event was described as extreme (Krishnan et al. 2011), and monitoring of 55 sites revealed bleaching of 70%–90% of corals across massive, branching and foliose growth forms (Mondal et al. 2014). In 2011, some recovery of bleached corals was noted together with evidence of coral recruitment (Mondal et al. 2014). Extensive bleaching was also recorded in 2016 (Mohanty et al. 2017, McClanahan et al. 2019, 2020), with some species of branching *Acropora* being severely affected (Majumdar et al. 2018).

In Pulau Weh in northern Sumatra, the 2010 bleaching event had profound consequences with 94% of *Acropora*, 87% of *Pocillopora* and 15% of massive corals being recorded as recently dead in surveys during May/June 2010 (Guest et al. 2012, Bridge et al. 2014). In 2016, severe temperature-induced coral bleaching was noted on islands in Aceh province (Keith et al. 2018) and along the west coast of Sumatra (Corvianawatie et al. 2018, Giyanto et al. 2022), with recovery being much slower than that recorded on the east coast of Sumatra and central Indonesia (Giyanto et al. 2022).

In the Myeik Archipelago, Myanmar, reef surveys have been carried out in 2013, 2014, 2018, 2019 (Tun 2013, Howard et al. 2014, Obura et al. 2014, Howard 2018, Lunn et al. 2022) and 2022, 2023 (Z. Lunn – personal communication). Outer reef sites dominated by branching *Acropora* exhibited extensive mortality in surveys in 2013–2014, which was tentatively attributed to the earlier bleaching events of 2005 and 2010, though inner reef sites were much less affected and recovery here was aided by the fast growth of branching corals (Howard et al. 2014, Obura et al. 2014). No extensive bleaching was observed during surveys in 2016 though some limited bleaching was noted further north on reefs along the Mawdin coast of Myanmar (Murray-Jones et al. 2016). In 2022–2023, the reefs were in good condition with no evidence of coral bleaching (Z. Lunn – personal communication).

These coral bleaching events around the Andaman Sea are mirrored by plots (Figure 4) of Degree Heating Weeks (DHW) (a measure of accumulated heat stress in °C-weeks) (Liu et al. 2014) for 5 km grid squares closest to sites where reef monitoring has taken place over time. Based on research at Coral Reef Watch (https://coralreefwatch.noaa.gov/product/5km/tutorial/crw10a_dhw_product.php), when DHW reaches 4°C-weeks, coral bleaching is assessed as likely, especially in more sensitive species; when DHW approaches 8°C-weeks, widespread bleaching and significant coral mortality are likely to occur. While there are limitations in the use of DHW as a metric for bleaching (Wyatt et al. 2023) and occasions where slight modification is needed for areas where it does not accurately reflect the temperature stress encountered (Guest et al. 2012), it nonetheless provides a useful comparator for evaluating temperature stress in this region. In particular, the severe bleaching event of 2010 was accompanied by the highest DHW at all locations, while in 2016, severe heat stress was most obvious at Aceh and in the Andaman Islands, with the least heat stress in the Myeik Archipelago, where observed bleaching was minimal.

An important factor limiting the bleaching susceptibility of corals in the turbid inshore reefs of Myanmar, Thailand and the Andaman and Nicobar Islands is the reduced penetration of solar radiation in these waters (Dunne & Brown 1996, Brown et al. 2019). It is recognised that light is known to damage photosynthetic processes in coral symbiotic algae at elevated temperatures (Iglesias-Prieto et al. 1992, Fitt et al. 2001, Brown & Dunne 2016), and any reduction in light levels is clearly beneficial to corals living in turbid conditions when exposed to elevated SSTs during a bleaching event (Brown et al. 2019).

REVISITING THE CORAL REEFS OF THE ANDAMAN SEA

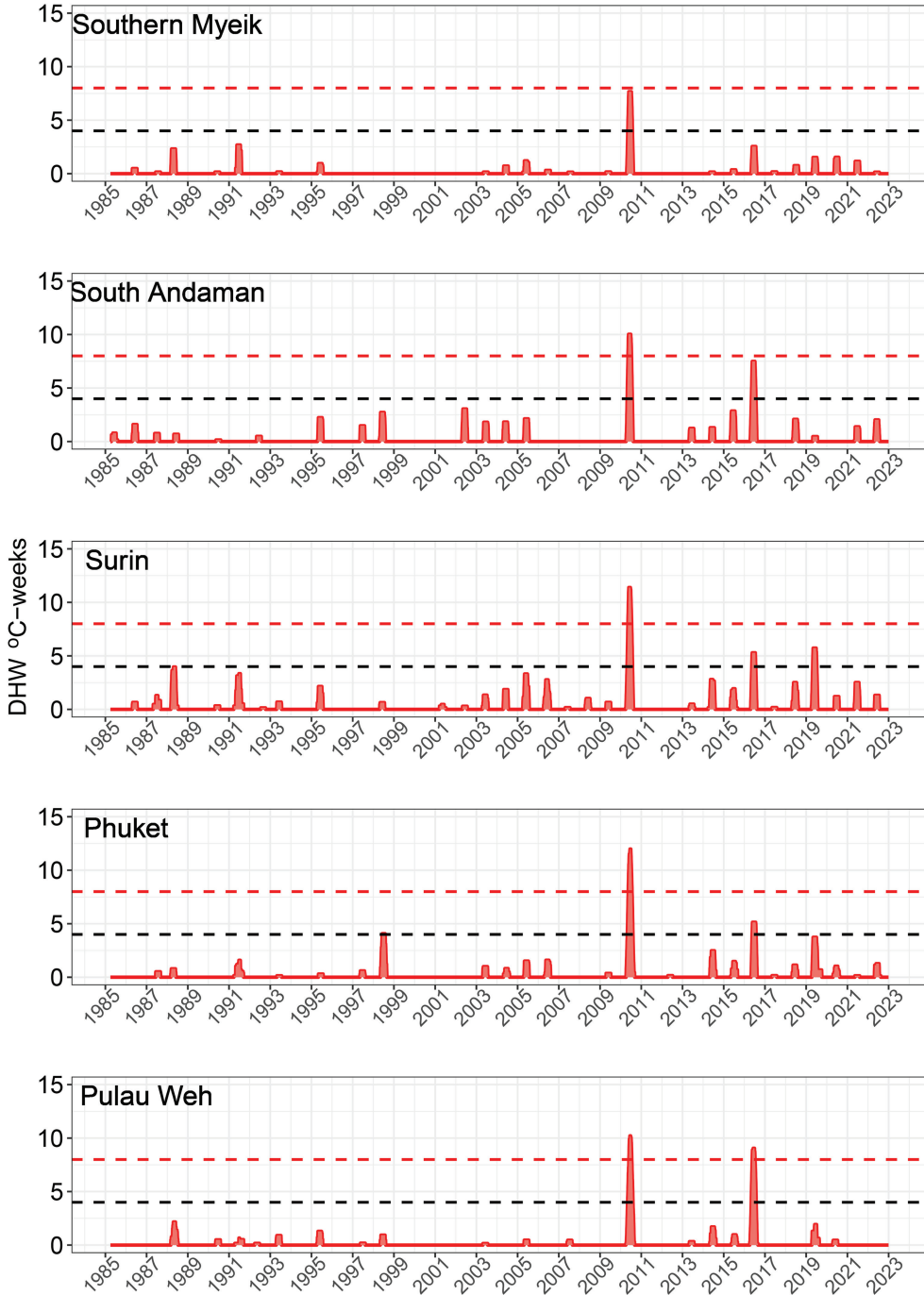


Figure 4 Degree Heating Weeks (DHW – °C-weeks) 1 April 1985–31 December 2022 for five 5 km² grid locations in the Andaman Sea (NOAA Coral Reef Watch 2018). Dataset accessed 6 March 2023 at https://pae-paha.pacioos.hawaii.edu/erddap/griddap/dhw_5km.html. Southern Myeik Archipelago (10.275°N 97.825°E grid centre), South Andaman Island (11.325°N 92.325°E), Surin Islands (9.425°N 97.775°E), Phuket (7.825°N 98.275°E) and Pulau Weh (5.875°N 95.025°E). The black dashed line=4°C-weeks and red dashed line=8°C-weeks. See Figure 1 for locations.

*Sea-level changes, El Niño Southern Oscillation
(ENSO) and Indian Ocean Dipole (IOD)*

Variability in mean sea-level in the Andaman Sea can be attributed to many causes, which include climate-related anomalous wind stresses, seasonal monsoonal effects, interannual ocean/atmosphere phenomena such as ENSO and IOD and vertical land movement resulting from tectonic activity.

Over the timescale of the satellite altimeter record (1993–present), the Equatorial and Northern Indian Ocean (ENIO) north of 5°S latitude, bounded on three sides by land masses, has exhibited considerable temporal and spatial variability in sea surface height trends. This variability has been attributed to mechanisms of wind-driven heat redistribution, namely wind stress at the equator, and deep upwelling (Thompson et al. 2016).

In the Andaman Sea, rates of absolute sea-level rise at Phuket have varied temporally from $3.37 \text{ mm year}^{-1}$ (1993–2011) (Brown et al. 2011) to $4.85 \pm 1.262 \text{ mm year}^{-1}$ (\pm SE) (1993–2016) (Brown et al. 2019) (Figure 5 shows this most recent trend). Other rates for Phuket computed using different methods include $3.88 \pm 0.45 \text{ mm year}^{-1}$ (1992–2018) (Simons et al. 2019) and $3.32 \pm 0.44 \text{ mm year}^{-1}$ (1992–2020) (Naeije et al. 2022). These computations of long-term trends in sea level are dependent on the time period analysed (Brown et al. 2011), and although the rates appear to differ, the 95% confidence intervals overlap, so any differences are more apparent than real.

Superimposed on long-term changes in sea level are other climate-related processes which act at seasonal and decadal/interdecadal time scales such as the reversing seasonal monsoons (Aparna et al. 2012, Han et al. 2018), ENSO (Bjerknes 1969) and IOD (Saji et al. 1999, 2018). Monsoon influences cause an annual seasonal depression of mean sea level of up to 20 cm during the dry season (November–April) (Brown et al. 1994), which has a significant impact on the length and timing of

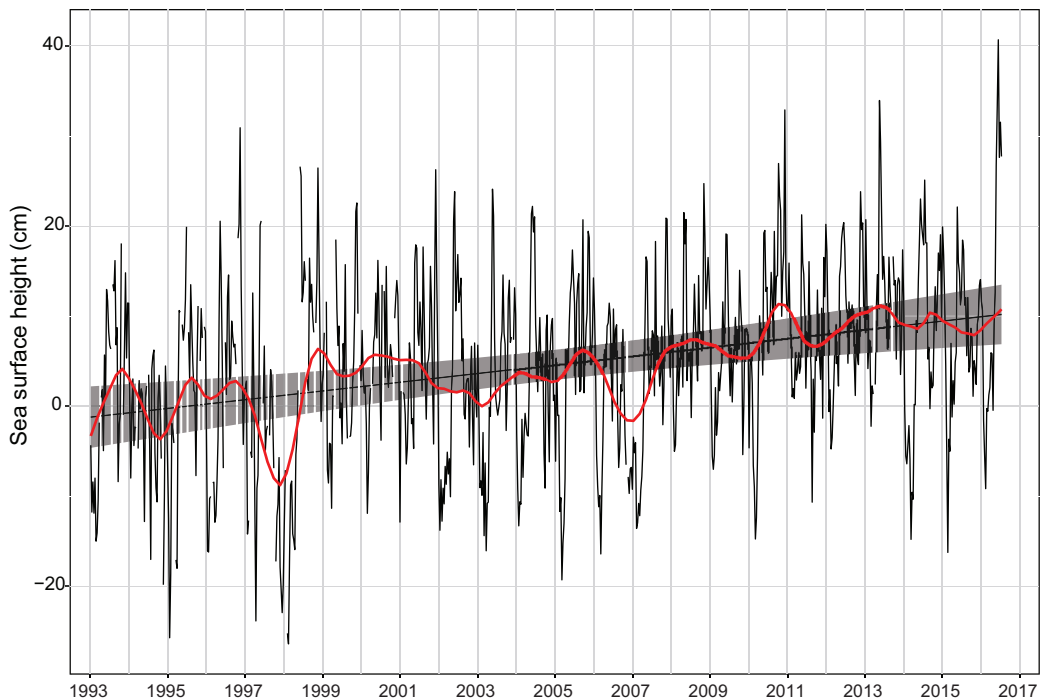


Figure 5 Satellite altimeter sea surface height anomalies for Phuket (98°E 7°N). Linear trend line (slope $4.85 \pm 1.262 \text{ mm year}^{-1}$ (mean \pm SE), Generalised Least Square AR4 model and 95% confidence intervals (grey shading) and Seasonal and Trend Decomposition using Loess trend (red line) (Brown et al. 2019).

aerial exposure for intertidal corals. Such a depression leads to a greater aerial exposure time, which affects all intertidal reefs, especially corals on macrotidal reefs on the coast of Myanmar, where the tidal range exceeds 4 m (Brown 2007). In addition, subtidal corals on the upper reef slopes along the Thai coast may also find themselves aerially exposed during low spring tides in the dry season (Brown & Phongsuwan 2004).

Both ENSO and IOD also have a major influence on SST and sea levels in the Andaman Sea. During ENSO years, SSTs are elevated in the region, potentially leading to extensive coral bleaching at the same time as sea levels are lowered (Dunne et al. 2021). Intertidal and subtidal corals suffer temperature-induced coral bleaching, while intertidal corals are also susceptible to stresses from aerial exposure because of depressed sea levels (Brown et al. 2019). The IOD is a mode of variability characterised by SST anomalies on the eastern and western sides of the Indian Ocean (Good et al. 2021). Positive IOD (*p*IOD) events are initiated by enhanced ocean upwelling along the coast of Sumatra, which generates cool SSTs in the east, resulting in strengthened easterly winds along the equator and enhanced warming, a lowered thermocline and reduced upwelling in the western Indian Ocean. In the Andaman Sea in the eastern Indian Ocean, SSTs are lowered at this time, while the thermocline is raised and upwelling enhanced. A negative IOD is characterised by anomalous westerlies over the tropical Indian Ocean, warming in the eastern basin, a raised thermocline and enhanced upwelling in the western Indian Ocean (Lu et al. 2018), while SSTs in the Andaman Sea are raised, the thermocline lowered and upwelling reduced. Simultaneously, during a *p*IOD, the sea level in the Andaman Sea is lowered, while in the western Indian Ocean, it is raised; during a negative IOD, the reverse occurs. A very marked sea-level depression occurred in the Andaman Sea during a strong *p*IOD in 1997, leading to significant mortality on intertidal reefs and shallow reef slopes around Phuket, where the sea-level depression lasted for over 8–10 months and at times exceeded 20 cm (Brown & Phongsuwan 2004, Brown et al. 2019). Similar sea-level depressions were noted at the time on the northwest coast of Sumatra where sea level was >30 cm lower for several months (Webster et al. 1999). Significant coral mortality was also noted in the Mentawai Islands on this coastline, and although surveys were not carried out at the time, subsequent analyses of *Porites* microatolls indicated die back in 1997 (Abram et al. 2003). These authors attributed the coral mortality to phytoplankton blooms caused by Indonesian wildfires though other workers doubted this as the sole cause (Hoeksema & Cleary 2004, van Woetik 2004). It is likely that the depressed sea level in 1997 and the related *p*IOD upwelling would also have played a role in the mortality, with the former having a major impact on shallow water corals.

Over the last 40 years (1979–2019), ENSO and IOD events have overlapped on occasions in the Andaman Sea. Such co-occurrences were in 1997, 2010 and 2019 when the largest reductions in intertidal coral cover over the 40 years period in the Thai-Andaman Sea were recorded (Figure 6) (Dunne et al. 2021). However, the nature of the events in 1997 and 2019, when *p*IODs were the most pronounced on record, was quite different. In 1997, elevated SSTs occurred 5 months after the lowered sea levels, while in 2019, elevated SSTs and lowered sea levels acted sequentially with high DHW lasting from May to July, immediately followed by falling sea level from July to December (Dunne et al. 2021). Generalised Additive Mixed Models (GAMM) identified that in 1997 sea-level depression was a major factor in the loss of coral cover, while DHW had a lesser effect. Conversely in 2019, the model showed that DHW contributed to coral cover reduction more than depressed sea level (Dunne et al. 2021).

Clearly, the interactions of these stochastic phenomena and their effects on coral reefs in the Andaman Sea are both complex and frequently damaging. Furthermore, several studies predict that the frequency and strength of both ENSO (Cai et al. 2022) and *p*IOD (Nakamura et al. 2009, Abram et al. 2020, Cai et al. 2021) will increase as the climate warms. Although the magnitude of sea-level depressions is expected to be reduced by future sea-level rise, SST increases associated with ENSO events and steadily warming background SSTs are likely to exacerbate warming episodes for corals in the Andaman Sea, which are already close to their thermal threshold (Dunne et al. 2021).

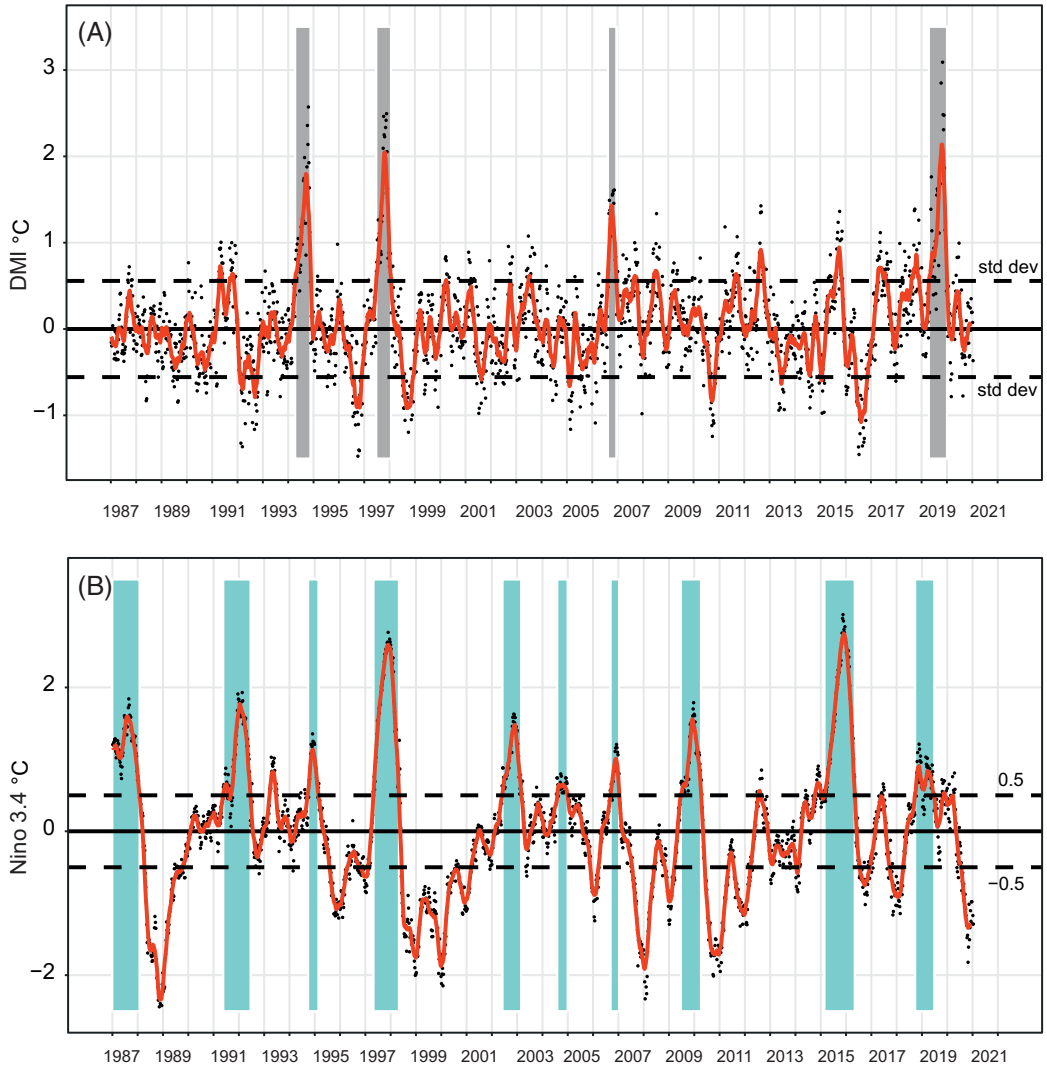


Figure 6 (A) Dipole Mode Index (DMI) and (B) Niño 3.4 Index (1987–2021). Black dots are weekly values, grey shaded time periods represent timing of *p*IOD (DMI > 0.56°C equivalent to 1 standard deviation) and cyan shading for El Niño events (Niño 3.4 > 0.5°C) (Dunne et al. 2021).

Seismic-induced temporal changes in land movement and their influence on coral reefs in the Andaman Sea

The complex geology of the Andaman Sea and its tectonic setting have been described elsewhere (Curry 2005, Khan & Chakraborty 2005, Brown 2007). Two major earthquakes in 2004 and 2005 along the Sunda arc, which marks the border of the Indian and Asian ocean plates to the west of Sumatra and the Andaman and Nicobar Islands, highlight the geological instability of the region and the implications for both humans and biological resources (Bilham 2005, 2006, Sieh 2005, Briggs et al. 2006, Tsang et al. 2015).

The effects of the December 2004 earthquake on the coral reefs in the Andaman Sea have been profound, impacting not only the Andaman and Nicobar Islands (Malik et al. 2006, Meltzner et al. 2006, Rajendran et al. 2007) and northern Aceh (Baird et al. 2005), but also the coastline of western Thailand (Brown et al. 2019, Simons et al. 2019, Naeije et al. 2022) and the islands of Myanmar (Meltzner et al. 2006). These effects were both immediate and long lasting, with changing sea levels, resulting from land uplift and subsidence, continuing to be experienced some 17 years after the earthquake (Satirapod et al. 2013, Simons et al. 2019, Naeije et al. 2022).

Immediately following the 2004 earthquake, dramatic changes to the landscape took place in the Andaman and Nicobar Islands with subsidence of ~1.5–2 m occurring along the coasts of South Andaman and the Nicobar Islands, vertical uplift in the order of 1.2 m on the east coast of North Andaman and uplift of up to 1–2 m on the west coast of Middle and North Andaman (Malik et al. 2006, Meltzner et al. 2006, Searle 2006, Rajendran et al. 2007). Subsidence caused major mortality of corals on shallow reefs in the Nicobar Islands through submergence and heavy sedimentation following the consequent tsunami. Similarly, high coral mortality occurred on the extensive uplifted intertidal reef flats on western coasts of the Andaman Islands through aerial exposure (Patterson et al. 2006, Jeyabaskaran & Rao 2007, Bahuguna et al. 2008, Saxena et al. 2008, Majumdar et al. 2018) (Figure 7). In the Nicobars, it was estimated that of a total area of reef of 223.7 km² before the earthquake, only 10 km² remained afterwards (Bahuguna et al. 2008), while tens of km² of intertidal reefs were lost on the west coasts of the Andaman Islands (Brown 2005). At the northern tip of North Andaman lies Preparis Island which belongs to Myanmar. Here, a minor uplift of 20–30 cm



Figure 7 Fringing coral reef at Interview Island off the west coast of Middle Andaman Island, where the reef had been uplifted by 2 m following the 26 December 2004 earthquake, leaving the reef permanently stranded above the present-day high tide. (Photo credit: Mike Searle.)

was estimated to have occurred as a result of the earthquake (Meltzner et al. 2006), but there are no records of any effects on coral reefs from this location.

Throughout the region, the tsunami that followed the earthquake had varying impacts on the coral reefs. Since actual wave heights over the reefs bordering coastlines were difficult to calculate, estimations of tsunami run-up (the tsunami height above mean sea level at its limit of penetration inland) at different locations provide a useful comparator (Spencer 2007). These were high at sites closest to the earthquake such as Pulau Weh in northern Sumatra (3.02–6.2 m), at Great Nicobar (3–6 m) and at South Andaman (2.9–4.5 m) (Spencer 2007). The highest of all was Khao Lak (4.48–9.91 m) on the northern Andaman Sea coast of Thailand where wave height was amplified by the extensive shallow continental shelf offshore. Lower tsunami run-ups of 1.5–5.5 m were recorded for Middle and North Andaman and Phuket on the west coast of Thailand (Spencer 2007).

Surprisingly, the effects of the tsunami on many coral reefs in the Andaman Sea were minimal. At Pulau Weh and along the west coast of Aceh, North Sumatra, the effects were patchy with most of the damage occurring at depths <10 m where colonies were broken, overturned or suffered from sedimentation (Baird et al. 2005, Gunawan et al. 2006, Campbell et al. 2007, Hagan et al. 2007). Similar effects were described along the Thai-Andaman Sea coast where only 13% of sites were seriously damaged, with 47% showing low to moderate impacts and 40% appearing undamaged (Phongsuwan et al. 2006, Phongsuwan & Brown 2007). In the Andamans, the effects of the tsunami were described as ‘not very pronounced’ (Saxena et al. 2008), but in the Nicobar Islands, where wave heights of 10–15 m were recorded, there were mass mortalities of corals due to bleaching and increased sedimentation resulting from the tsunami (Patterson et al. 2006). Post-tsunami surveys across Nicobar reefs showed distinct distance-related impacts on coral size structure, with pronounced decreases in the abundance of large *Acropora* and *Porites* corals closer to the earthquake epicentre (Patankar et al. 2012). Minimal effects of the tsunami were reported from Myanmar, where surveys in 2005 in the southern islands of the Myeik Archipelago revealed a few overturned coral colonies, with others covered by a fine layer of sand (Tun & Heiss 2006). According to these authors, the tsunami wave had diminished to 0.5 m in height by the time it reached the coastline of Myanmar.

Longer-term effects of the earthquake on coral reefs were apparent on the Andaman Sea coast of Thailand, where over the period 2004–2021, there have been significant vertical land movements. Using Global Positioning System (GPS) data, satellite altimetry and tide gauge measurements, Naeije et al. (2022) showed that at Phuket a vertical land drop of ~10 cm occurred over this period (Figure 8), which resulted in a relative sea-level rise of up to 16 cm. As Figure 8 shows, post-seismic disturbance is now diminishing though vertical velocity estimates indicate that slight tectonic subsidence is still ongoing. Such changes in sea level have implications for both intertidal and subtidal

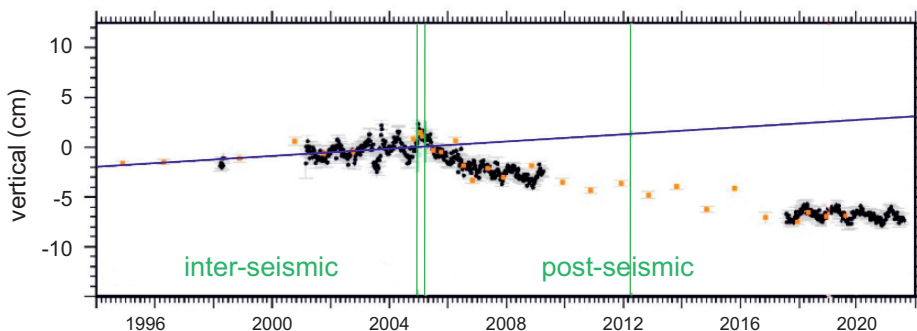


Figure 8 Vertical displacement (cm) of Phuket island as monitored from a combined station GPS position time series (black data points \pm SE). The inter-seismic (1994–2004) velocity estimates and trend line are shown in blue (2.35 ± 0.21 mm y⁻¹). The orange dots mark the position solutions from the yearly PHUK (3–7 days) GPS surveys. Green vertical lines mark the 2004, 2005 and 2012 earthquakes originating from the Sumatra Trench (Naeije et al. 2022).

reefs. For intertidal reefs, more ‘accommodation’ space is made available for growth (Scopelitis et al. 2011, Saunders et al. 2015, van Woessik et al. 2015) as well as greater flushing (Nakamura & van Woessik 2001, Nakamura et al. 2003) and slightly deeper water with less light penetration during temperature-induced bleaching events (Cacciapaglia & van Woessik 2016). Shallow subtidal reefs also benefit from improved flushing and reduced light penetration.

For intertidal reefs around south-east Phuket, relative sea-level rise over the period 2004–2010 resulted in sustained high coral cover on the mid and outer reef flats (Brown et al. 2011). A severe temperature-induced coral bleaching event in 2010 then caused cover to decrease dramatically, but the continued rise in sea level has contributed to a rapid recovery of the reefs up to the present day (Brown et al. 2019, Dunne et al. 2021). Further north at Ranong, which is close to the Thai border with Myanmar, between 2004 and 2020, relative sea-level has risen 22 cm as a result of the vertical post-seismic subsidence following the 2004 Sumatran earthquake (Naeije et al. 2022). If, as is likely, the intertidal and subtidal reefs in the nearby southern Myeik Archipelago have also experienced similar changes in sea level, then this may provide a contributory factor to increases in coral cover recorded between the first surveys in 2014 and later resurveying in 2018 (Lunn et al. 2022).

Large amplitude internal waves (LAIWs) and surface waves and their influence on coral reefs in the Andaman Sea

The Andaman Sea has long been recognised as an area where there is an interaction between surface and internal waves. In his book on the Physical Geography of the Sea, Maury (1860) reported observations by the hydrographer James Horsburgh first recorded in the 1817 edition of his East India Directory (Horsburgh 1817):

The Rippings are seen in calm weather approaching from a distance, and in the night their noise is heard a considerable time before they come near. They beat against the sides of a ship with great violence, and pass on, the spray sometimes coming on deck; and by carrying out oceanographic measurements from a ship, a small boat could not always resist the turbulence of these remarkable Rippings.

Maury (1860, p. 389)

Internal waves form as a result of disturbances within a layered ocean. Differences in density and salinity cause the layers to act as different fluid masses, and when tides, currents, gravity and Earth’s rotation move these over complex seafloor topography, internal waves are created. West of the Andaman and Nicobar Islands, the Indian Ocean seafloor rises steeply from 3000 to 200 m around the islands and then falls again within the Andaman Sea. In this western sector of the Andaman Sea, the irregular bottom topography consists of shallow ridges, reefs and submarine banks, which alter the flow of water as it moves in and out of the basin. It is in this area that the internal waves are generated by the interaction of the baroclinic tide with the shallow bottom features (Osborne & Burch 1980, Alpers et al. 1997).

Internal waves in the Andaman Sea have variously been described as internal tides (Mohanty et al. 2018, Peng et al. 2021, Yadidya & Rao 2022), internal solitary waves (Magalhaes & da Silva 2018, Magalhaes et al. 2020, Sun et al. 2021) and LAIW (Wall et al. 2015). In this account, we shall refer to the internal waves as LAIW since this term has been extensively used in coral reef literature based on work in the Andaman Sea. LAIW are tidally generated along the underwater ridges of the Andaman and Nicobar Islands, which then propagate eastwards, retaining their speed and shape for considerable distances with a decreasing velocity as they move from deep to shallow water (Mohanty et al. 2018). Travelling at speeds of 2–3 m sec⁻¹ in packs of 5–7 waves, they can depress the thermocline by as much as 80 m (Osborne & Burch 1980, Sun et al. 2021). A unique feature of internal waves generated in the Andaman Sea is that they are not generated from a single site unlike

in the South China Sea and Sulu Sea (Yang et al. 2021b), but from multiple locations (Magalhaes & da Silva 2018, Mohanty et al. 2018, Jensen et al. 2020, Raju et al. 2020, Sun et al. 2021, Yang et al. 2021b). Five possible generation sites (**A–E** in Figure 9A) have been identified from satellite imagery. Sites A and B lie northeast of the Andaman Islands, sites C and D in the Nicobar Islands and site E in the Great Channel above the northern tip of Sumatra (Raju et al. 2020). Internal waves from A, B and E propagate in a single direction, while those at C and D travel in two directions, with internal waves generated at Site A propagating in a southwest direction on the continental shelf of the eastern side of the Andaman Islands, waves from B travelling towards the northeast of the Andamans and on to the continental shelf of Myanmar and waves from site C travelling both east and west with those travelling west to the Bay of Bengal and eastward waves heading for the shelf of Myanmar and Thailand. Waves generated at site D appear to be refracted to the northeast with waves generated at site E travelling along the shallow shelf towards Thailand and the Malacca Strait. While the waves hitting the continental shelf become modified, it is also clear that there is interaction between wave trains with waves generated at sites D and E crossing paths with waves generated at C (Raju et al. 2020). A NASA Landsat image (Figure 9B) dated 29 November 2019 shows internal waves approaching the Myeik Archipelago, Myanmar. It is clear from Figure 9A that most reefs in the region, apart from those on the west sides of the Andaman Islands, are influenced to some degree by LAIW.

The highly complex internal wave regime is further complicated by the types of waves generated, which have now been identified as belonging to different types or modes (Magalhaes & da Silva 2018, Magalhaes et al. 2020, Yang et al. 2021b). In the Andaman, Sea Mode 1 and Mode 2 waves have been identified, with Mode 2 waves having a smaller amplitude than Mode 1 and each having different current and thermal structures (Magalhaes & da Silva 2018, Magalhaes et al. 2020). Mode 1 waves are described as depression waves, which switch to non-linear waves of elevation on approaching shallow water, while Mode 2 waves are elevation waves (Jackson et al. 2013). Elevation waves bring colder and deeper water to the surface and produce strong variations of SST around coral reefs in their path, lowering SST in periodic pulses as they approach the coast. Such effects are evident in the hourly temperature record from Ao Mayai in the Surin Islands (Figure 2). Similar dramatic temperature fluctuations have been detected around reefs on the west coasts of islands in the Thai-Andaman Sea, stretching from the Surin Islands in the north to Ko Racha in the south (Wall et al. 2015). In the Similan Islands, the strong vertical mixing and overturning of water associated with the internal waves have been shown to not only affect SSTs but also bring changes in pH and nutrient concentrations (Roder et al. 2010, 2011). Similar features have been observed at Dongsha Atoll in the South China Sea (Reid et al. 2019, Hung et al. 2021).

While LAIW exert their greatest influence on local oceanography during the dry season (January–April), strong wave action from monsoon-related surface waves is experienced by westerly facing coral reefs in the wet season (May–October) (Schmidt et al. 2012). These surface waves result in turbulent mixing and resuspension of sediments in shallow water, which in turn lead to reduced light intensities and smothering of corals (Wall et al. 2012). Additional mixing, turbulence and upwelling in the water column of the Andaman Sea result from mesoscale cyclonic eddies, which can be between 10 and 500 km in diameter and persist for days or months (Buranapratheprat et al. 2010, Cui et al. 2016). Modelling studies suggest that the Andaman and Nicobar Islands play an important part in their generation (Mukherjee et al. 2019)

The existence of LAIW, monsoon-related surface waves and mesoscale eddies thus makes the Andaman Sea a highly dynamic physical environment. The effects of LAIW and surface waves on coral reefs in the region have only been documented for islands in the Thai-Andaman Sea where LAIW, through strong wave action, SST depressions and increased nutrients, have been described as reducing reef framework and coral diversity (Schmidt et al. 2012, Wall et al. 2012) but increasing turf algae cover (Jantzen et al. 2013) on the exposed western sides of islands compared with

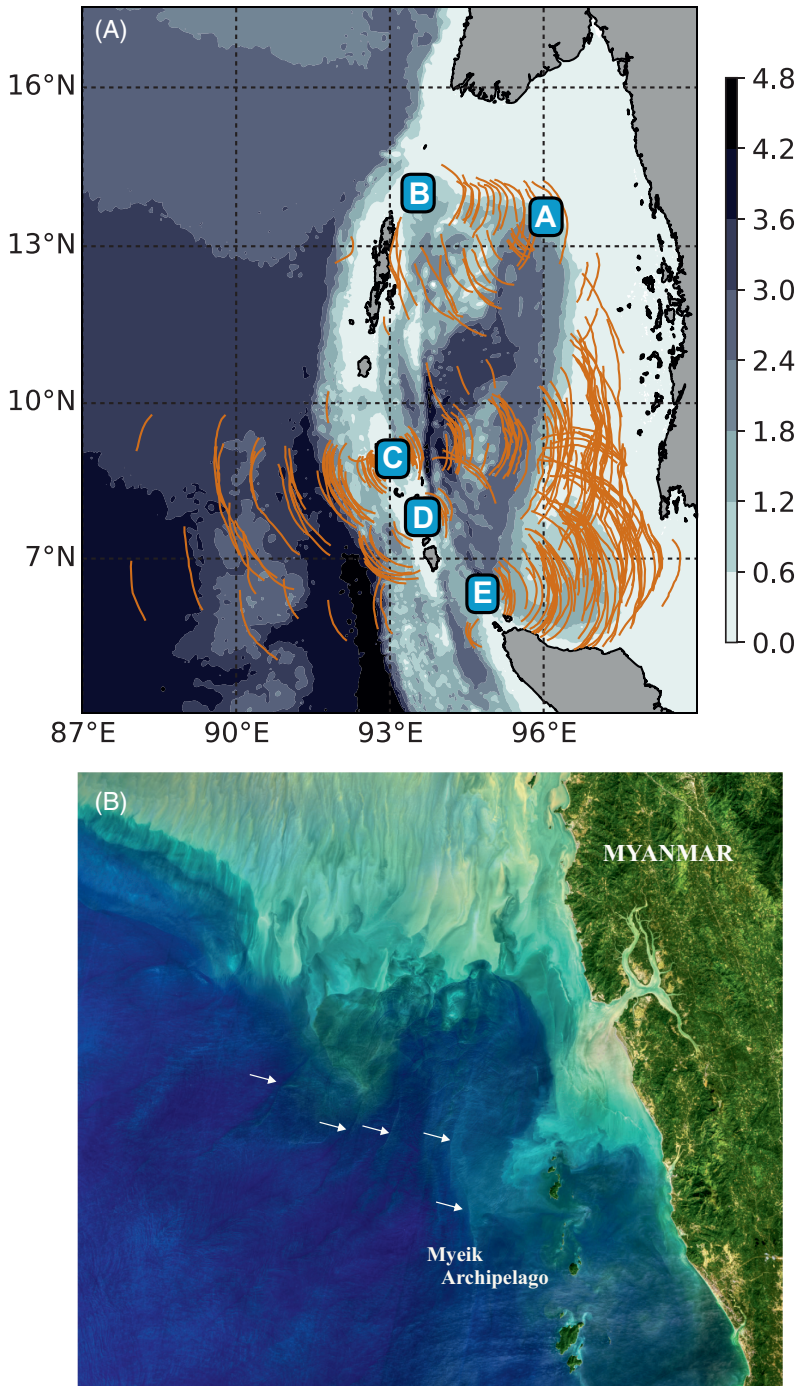


Figure 9 (A) Map of all the leading waves in each solitary wave packet in the Andaman Sea, as observed in the Moderate Resolution Imaging Spectroradiometer (MODIS) satellite imagery during the months of March–April from 2014 to 2016. Lettering indicates possible generation sites of internal solitary waves (Raju et al. 2020). (B) Internal waves (indicated by arrows) approach the Myeik Archipelago, Andaman Sea in an image from the Operational Land Imager on Landsat 8 on 29 November 2019. (Reproduced with the permission of NASA Earth Observatory.)

the sheltered east sides. Studies have also revealed an increase in host and symbiont biomass in the corals *Porites lutea* and *Diploastrea heliopora* from western-facing reefs in the Similans (Roder et al. 2010), while *Pocillopora meandrina* from western reefs appeared to be more heterotrophic compared with colonies from eastern facing reefs (Roder et al. 2011). Improved coral bleaching resilience was also noted on western reefs on a number of islands in the Andaman Sea, compared with those with an easterly aspect, during the intense bleaching event in the region in 2010 (Wall et al. 2015, Schmidt et al. 2016), an effect likely related to the finding that high-frequency temperature variability appears to reduce susceptibility to coral bleaching (Thompson & Van Woessik 2009, Oliver & Palumbi 2011, Safaie et al. 2018).

The LAIWs have also been implicated in causing reduced growth and linear extension in the dominant massive coral *P. lutea* on the western sides of islands in the Similans, where the effects of monsoon-induced surface waves and LAIW were evaluated on east- and west-facing island sites (Schmidt & Richter 2013). Earlier studies, which focused on an inshore–offshore gradient around Phuket but also included Ko Miang, a site in the Similans, had shown that linear extension decreased and bulk density of *P. lutea* skeletons increased along a gradient of increasing hydraulic energy. Coral skeletons from both Ko Miang and Ko Racha (a site to the south of Phuket) have lower linear extension, and those from Ko Miang have higher bulk density, than all other more sheltered locations that were not subject to such intense LAIW activity (Scoffin et al. 1992).

Interestingly, in a study of long-term changes of *P. lutea* growth at sites around Phuket from December 1984 to November 1986 and again from December 2003 to November 2005, a decrease in calcification and linear extension was observed at a number of sheltered sites but not at Ko Racha (Tanzil et al. 2009). Similarly, in a comparison of growth rates of *P. lutea* around the Thai-Malay peninsula between 1980 and 2010, decreases in calcification were noted in five out of six locations, the one exception being Ko Racha, the only site affected by LAIW (Tanzil et al. 2013). In this study, a significant link was observed between region-wide growth rates and average SSTs when Ko Racha was not included in the analysis because of its significantly different temperature regime and periodic pulses of anomalously cold water resulting from the LAIWs.

It is clear then that both coral reef ecology and coral physiology in the Thai-Andaman Sea are markedly affected by the highly dynamic physical environment around them, and it seems quite likely that fringing reefs on the east coast of the Andamans and the Myeik Archipelago of Myanmar might be similarly influenced.

Assessment of current reef condition in the Andaman Sea

Regional long-term coral cover datasets exceeding 15 years exist only for shallow subtidal coral reefs (5–12 m depth) in the Thai-Andaman Sea and at Pulau Weh in Aceh province, Sumatra, and for intertidal reefs around the southeast coast of Phuket, Thailand (Baird et al. 2005, Phongsuwan & Chansang 2012, Brown et al. 2019). Sporadic data on coral cover is available from 1996 to 2019 from shallow reefs surrounding four islands in the Mahatma Gandhi Marine National Park (MGMNP) in the South Andaman district of the Andamans Islands, while coral cover measurements from Myanmar are restricted to irregular repeated surveys between 2014 and 2023 at sites in the Myeik Archipelago.

Trends in coral cover data collected between 1988 and 2021 from 21 shallow (depth 5–12 m) subtidal sites in the Thai-Andaman Sea, stretching from the Surin Islands in the north to offshore and inshore reefs around Phuket in the south, are shown in Figure 10. Sites were selected on the basis that each dataset had been collected over at least a 25-year period and included surveys from the last decade up to 2021 (Phuket Marine Biological Center 2016, Marine and Coastal Resources Research and Development Institute 2020) and National Parks Operating Center – personal communication. While there is variability in coral cover between different sites, the depression in cover

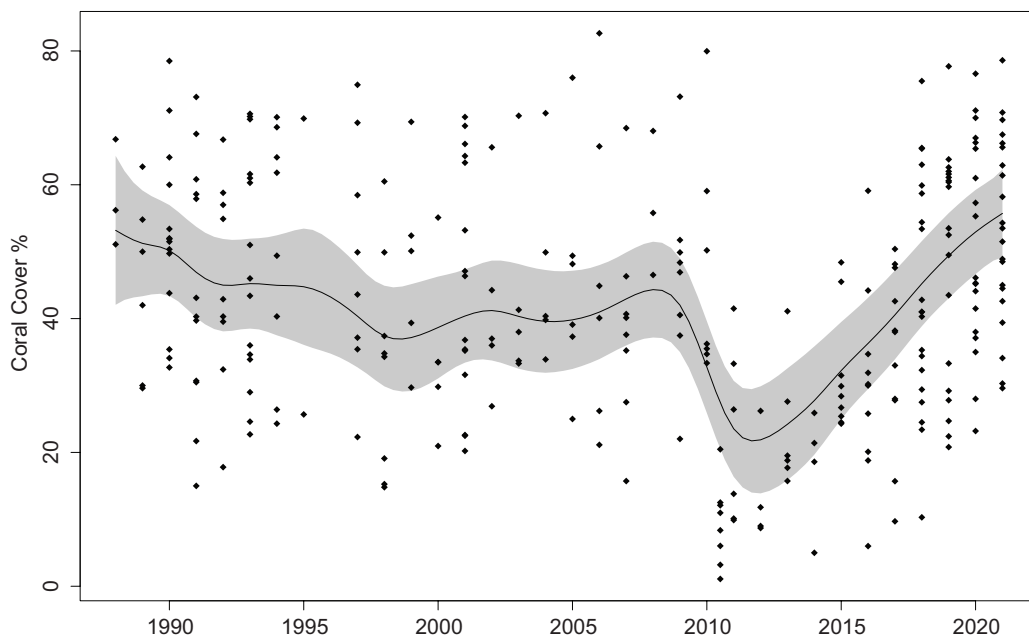


Figure 10 Long-term coral cover data (%) (1988–2021) from 21 subtidal sites in the Thai-Andaman Sea (black dots). Trend line (GAMM AR1) with 95% confidence intervals (grey shading). Data from Phongsuwan and Chansang (2012), Phuket Marine Biological Center (2016), Marine and Coastal Resources Research and Development Institute (2020) and National Park Operating Center, Thailand – personal communication.

following the 2010 bleaching event, which resulted in dramatic coral mortality, is clear, followed by live cover recovering significantly over the last decade to values comparable with those recorded in the early 1990s. This increase in coral cover in recent years has also been accompanied by marked changes in coral assemblage structure at several subtidal sites, which include an increase in the dominance of *Porites rus* over *Acropora* species and the persistence and increase in cover of bleaching tolerant species such as *Diploastrea heliopora* and *Heliopora hiberniana* (Phongsuwan & Chansang 2012, Taninaka et al. 2021).

The intertidal reefs around Phuket have shown similar recent trends in coral cover to the subtidal reefs, with a steady increase up to 2017 after the damaging 2010 bleaching event (Figure 11). For these reefs, however, there was also a decline in cover between 2018 and 2020 due to the effects of lowered sea level and increased SST as a result of the combined influences of *p*IOD and ENSO (Dunne et al. 2021). Since 2021, the intertidal reefs have shown a rapid recovery with coral cover values approaching those recorded in 2017. In previous years, these reefs have experienced mixed fortunes, with coral mortality when sea levels were lowered in 1997 during a marked *p*IOD, thriving coral growth in the early 2000s due to the lack of negative sea level anomalies and subsequently elevated sea levels when land subsided following the 2004 Sumatran earthquake (Brown et al. 2019). No changes in coral assemblage structure were noted following the 2010 bleaching event when coral cover decreased.

On the Myanmar coastline, the most detailed coral reef studies have been those around islands in the Myeik Archipelago, where a recent summary of the status of subtidal reefs recorded slight increases in coral cover between 2014 and 2019 (Lunn et al. 2022). The improved condition of surveyed reefs was maintained in 2022–2023 (Z. Lunn – personal communication). The inner reefs, like many sites throughout the Andaman Sea, are often turbid because of river run-off, with inner reef locations having an average coral cover of 55% and higher coral mortality from river drainage

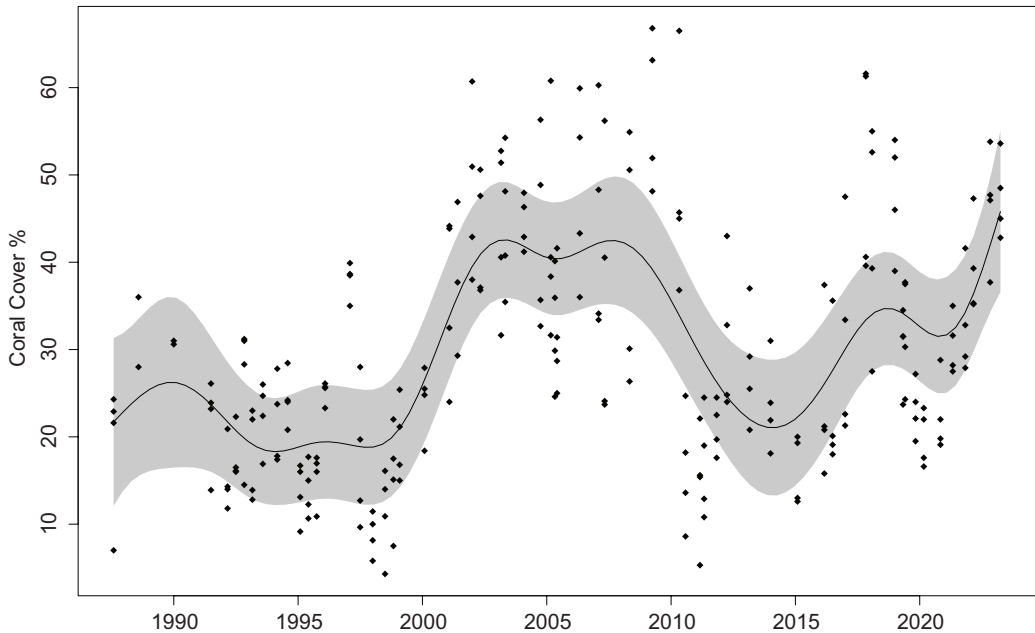


Figure 11 Live coral cover (%) (1986–2023) on four permanent belt transects on an intertidal reef flat at Phuket, with cover displayed as individual sampling points for each of the transects. Trend line (GAMM AR1) with 95% confidence interval (grey shading).

than at deeper depths (up to 10 m) further offshore (Howard 2018). There are examples of intertidal reefs of the Myeik Archipelago in early 2019, which appeared to be in good condition, like those in the Thai-Andaman Sea, where sheltered bays support a high cover of staghorn *Acropora* (Figure 12). Subsequently, anchor damage has been noted at Langann Island in the Myeik, but anchoring buoys have now been installed at this site to mitigate damage (Z. Lunn – personal communication). At Ao Koong in the Thai-Andaman Sea, the intertidal reef suffered considerable mortality because of lowered sea levels and increased sea temperatures due to *pIOD* and elevated SSTs in 2018–2020, but by 2022, the reef showed significant recovery (N. Phongsuwan – personal communication) (Figure 12B).

Coral disease is evident on coral reefs throughout the Myeik Archipelago at a level of 4%, which has been described as a similar figure to other Asia Pacific countries (Howard 2018). The greatest incidence of disease is found close to villages often where there was evidence of past dynamite fishing and discharge of untreated sewage. Plastic waste has been hypothesised to increase the susceptibility of corals to disease at these sites (Lamb et al. 2018). Diseases noted include skeletal eroding disease, brown band, black band, yellow band and white syndrome (Howard 2018). Coral disease surveys of *Porites lutea* immediately following the 2010 bleaching on reefs throughout the Thai-Andaman Sea revealed five disease categories, namely white syndrome, ulcerative white spot, focal and non-focal bleaching and pink spot (the latter described as a pigmentation response in surveys in the Myeik Archipelago) (Putchim et al. 2012, Howard 2018). Recent surveys of pigmentation responses in *P. lutea* around Okinawa, Japan, recorded a high incidence of pigmentation responses and tentatively linked their occurrence with the presence of epibionts (Kubomura et al. 2021).

Coral reef monitoring in the Andaman and Nicobar archipelago has not been as systematic or as frequent as that in the Thai-Andaman Sea, and the data shown in Figure 13 has been compiled

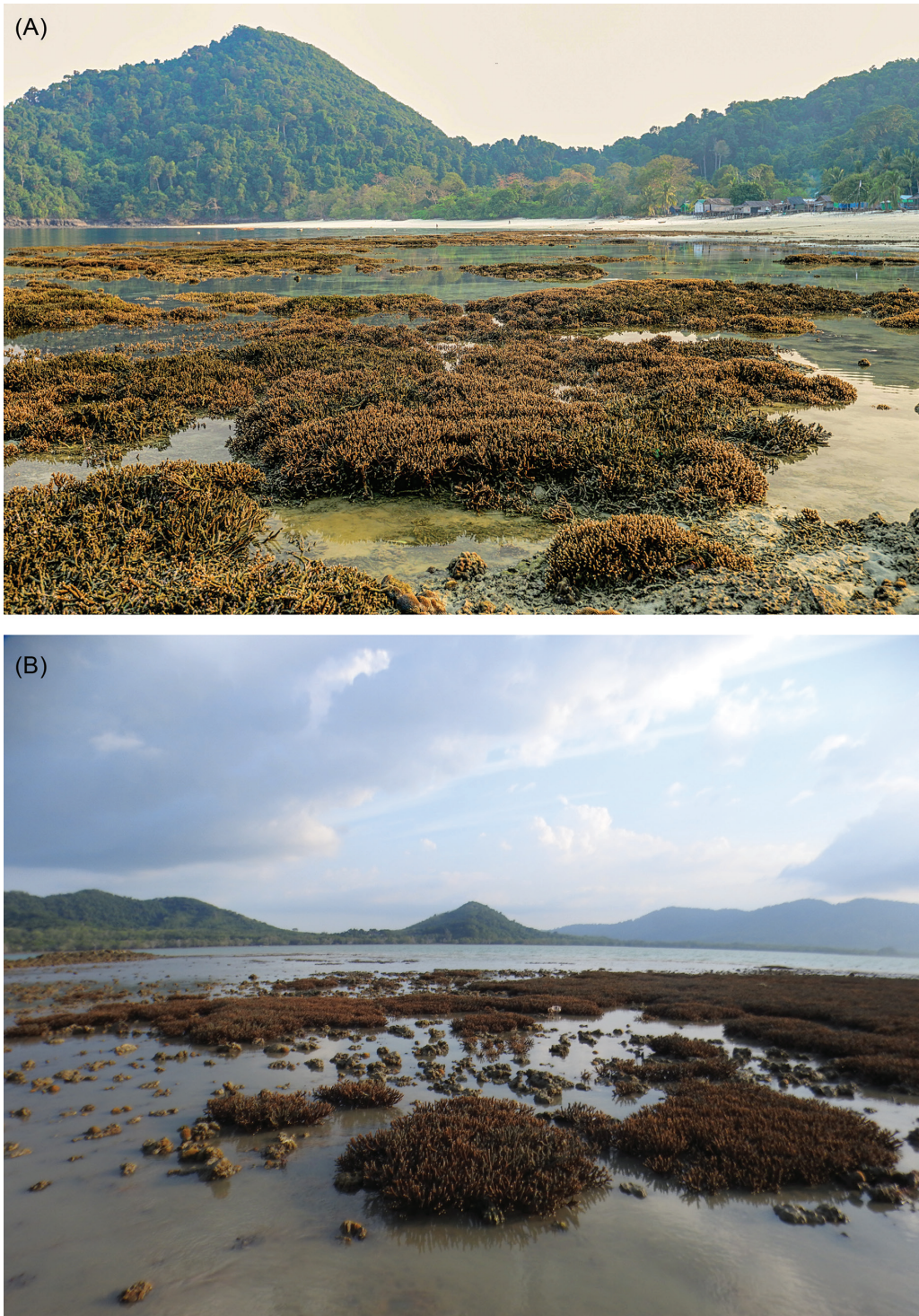


Figure 12 Thriving intertidal reefs photographed in early 2019 at (A) Langann Island, Myeik Archipelago, Myanmar (Photo credit: Rob Howard, Fauna and Flora International) and (B) Ao Koong, Phuket Island. (Photo credit: Saisanit Phongsuwan.)

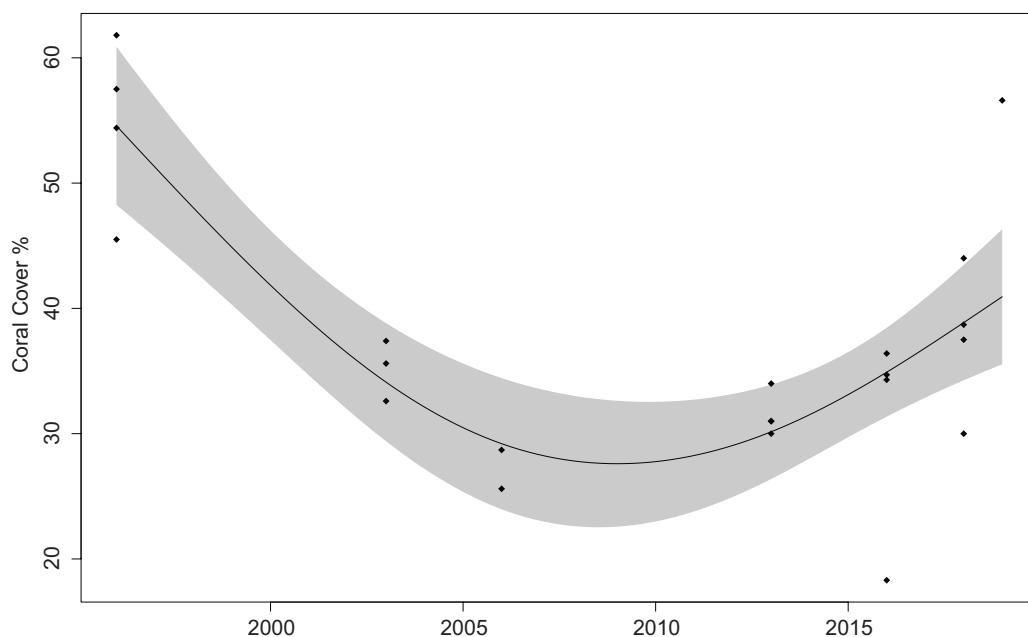


Figure 13 Long-term coral cover data (%) (1996–2019) from 4 subtidal sites in the Andaman Islands (black dots). Trend line (GAM) with 95% confidence intervals (grey shading).

from reef surveys on a group of islands in the MGMNP in the South Andamans. Here, coral cover was analysed from sites with a comparable depth (5–15 m) and aspect that had been surveyed at least three times within the last three decades. The earliest surveys in 1996 recorded relatively high coral cover (~54%) across shallow locations within the national park, where reefs were dominated by *Acropora* species, with arborescent *Acropora* species often being monodominant at some reef sites. By 2003, cover had already decreased significantly and continued to do so after the 2004 tsunami, reaching less than half the 1996 cover by 2006. The decline by 2003 could possibly be due to coral bleaching events in 1998 and 2002, where minor coral mortality was recorded from other parts of the archipelago (Pet-Soede et al. 2000, Krishnan et al. 2011). While bleaching and subsequent high coral mortality were observed on other reefs in the Andaman Islands during the 2010 ENSO (Krishnan et al. 2011, Marimuthu et al. 2013), it is difficult to evaluate how reefs in the MGMNP responded since no coral cover data exists for these sites during that event. However, by the time the reefs were surveyed in 2013, many were showing signs of recovery, and by 2019, coral cover was significantly higher (~40%) although not back to the 1996 baseline. Elsewhere in the archipelago, reef assessments have been scattered in their distribution, but overall, the Andaman Island reefs have fared relatively well over recent time, either escaping ENSO warming events completely or showing a patchy response (Marimuthu et al. 2013, Majumdar et al. 2018, McClanahan et al. 2020).

Surveys in the Acehnese Andaman Sea began in March 2003 at three shallow sites on Pulau Weh (depths 1–2 m). Mean coral cover was high at all sites ranging from 38.7% to 47.7% (Baird et al. 2005). Surveys in March 2005, 3 months after the Indian Ocean Tsunami, demonstrated that coral cover and assemblage structure had changed very little at these three sites, suggesting that direct damage to the reef from the tsunami was minimal (Baird et al. 2005, Campbell et al. 2007). Coral cover was also high, but variable at an additional six sites on Pulau Weh surveyed in March 2005 (Baird et al. 2005). The variation in coral cover among sites on Pulau Weh was correlated

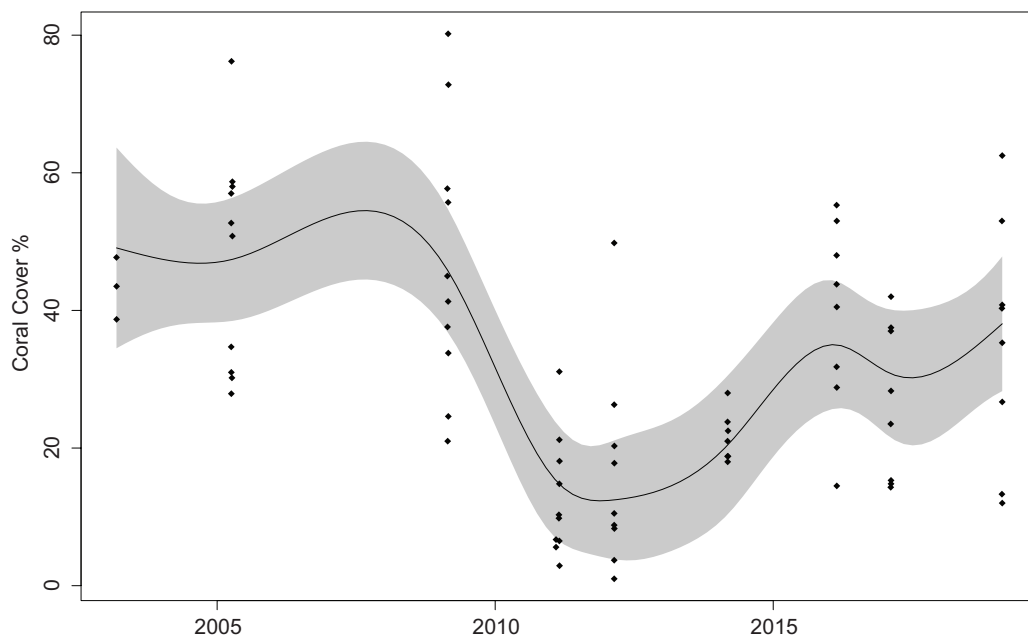


Figure 14 Long-term coral cover data (%) (2003–2019) from 12 subtidal sites (1–2m depth) around the island of Pulau Weh, Sumatra (black dots). Trend line (GAMM AR1) with 95% confidence intervals (grey shading).

with the types of fishing gear being used; in particular, the coral cover was low in areas where the use of fishing nets was permitted (Campbell et al. 2012). Sites on Pulau Weh were not typical of other sites in the region in 2005, such as the Pulau Aceh group to the north-west and sites on the west coast of the Sumatran mainland, where coral cover was uniformly low, a feature attributed to destructive fishing and inappropriate coastal development (Baird et al. 2005, Campbell et al. 2007). Regular surveys on Pulau Weh since 2005 suggest that the major cause of coral loss in the region is now the result of global warming, rather than direct human disturbance, with bleaching-induced mortality evident in 2010 and 2016 (Figure 14). The 2010 bleaching event was particularly severe with a significant decline in percent cover between 2009 and 2011 (Figure 14, see also Fadli et al. 2012). Since 2011, coral cover has gradually increased, with a slight decline recorded between 2016 and 2017 (Keith et al. 2018), although coral cover has yet to return to levels documented in 2003 (Figure 14).

Anthropogenic threats other than climate change

Some of the variability detected in reef surveys of coral cover in the region are likely due to anthropogenic influences other than climate change. Human influences on coral reefs in the Thai-Andaman Sea were briefly described in Brown (2007). Common threats throughout the region now include sedimentation from coastal development, plastic waste, damaging fishing practices particularly in Aceh (Baird et al. 2005) and Myanmar (Lunn et al. 2022), discarded fishing gear in Thailand (Phongsuwan et al. 2013) and Myanmar (Howard 2018, Lunn et al. 2022), over-fishing in the Andaman and Nicobar Islands, an increase in tourist-related damage on shallow reef areas in Thailand and the Andamans and Nicobar Islands (Phongsuwan et al. 2013, Mondal et al. 2014, Majumdar et al. 2018) and nitrogen pollution in the Andaman and Nicobar Islands (Painter et al. 2023).

While mechanisms need to be put in place to curb damage from such local threats, it is important to recognise that the preservation of coral reef habitats must take precedence over any reef restorative measures, with reef restoration considered as a poor replacement for adequate management of reef systems (Edwards 2010). For example, considerable damage from tourism activities such as boat anchoring, sewage discharge and novice diving activities was noted in 2013–2014 on reefs in the Khai Islands, east of Phuket, but once management regulations (including strict law enforcement, installation of mooring buoys and reef zonation for multiple use) were put in place in 2016, natural reef recovery was obvious after 3–4 years (N. Thongtham – personal communication).

Nonetheless, in Thailand, small-scale reef rehabilitation has been effective in restoring coral cover to a reef area damaged by a severe storm in 1986 on Maiton, a resort island near Phuket where little coral colonisation had taken place up to 1994 either because of poor coral recruitment and/or substrate instability (Yeemin et al. 2006, Thongtham & Chansang 2008). Substrate at the site was stabilised in 1994 by planting triangular prism modules, composed of concrete pipes of varying diameter, on the reef (Edwards 2010). Initial natural coral colonisation over the period 1994–2001 resulted in 53%–60% of the module surfaces being covered by live corals. Together with successful transplantation and survival of *Porites lutea* fragments between 2005 and 2008, an increase in the percentage of living coral from 10% (pre-restoration) to ~60% cover in 2016 and up to ~80% cover between 2018 and 2022 was noted (N. Thongtham – personal communication). The rehabilitation, however, did not result in restoring the original community structure, which had been dominated by *Acropora* species susceptible to storm damage, but rather it led to a more mixed community dominated by *P. lutea*. No doubt a contributing factor in this successful reef rehabilitation would have been the natural improvement in coral cover over recent time in the Thai-Andaman Sea, as noted in the previous section of this review.

The Andaman Sea as a mosaic of refugia for corals, physiological coral defences and possible limitations on coral resilience in these areas

Refugia

The term ‘coral refugia’ has been variously applied to reef sites within the Andaman Sea in recent years (Brown 2007, Wall et al. 2015, Bachman et al. 2022, Liu et al. 2022). Refugia have been defined as areas that support reef coral populations and to which reef corals can retreat to, persist in and subsequently expand from under changing environmental conditions (Keppel & Wardell-Johnson 2012, Cacciapaglia & van Woesik 2016). Kavousi & Keppel (2017) further maintain that coral refugia are environments subject to long-term buffering of environmental conditions with respect to climate change.

In the context of the Andaman Sea, Brown (2007) first used the term in a geological sense referring to turbid inshore habitats such as those that occur along the Thai/Myanmar coastline and around the Andaman and Nicobar Islands as refugia during non-optimal periods of reef growth from which corals might subsequently radiate out to more ‘typical’ oceanic habitats once environmental conditions have improved, as discussed by Potts and Jacobs (2000). Such turbid habitats in other parts of the world have also been identified as modern-day refugia since turbidity and resultant lowered light levels reduce the susceptibility of corals to bleaching at elevated sea temperatures and are clearly beneficial for those coral species preadapted to these environments (Cacciapaglia & van Woesik 2016, Sully & van Woesik 2020). The shallow reefs on the Thai/Myanmar coastline exist in highly turbid waters (Brown 2007, Howard 2018) where sedimentation rates of 120 kg m⁻² year⁻¹ have been reported around inshore sites in the Thai-Andaman Sea (Tudhope & Scoffin 1994) and

where light levels over the reef are rapidly attenuated (Dunne & Brown 1996), so helping to mitigate the effects of rising sea temperatures (Fitt et al. 2001) in corals tolerant of a high sediment regime.

Thermal refugia have also been identified in the Andaman Sea at sites that are strongly influenced by internal waves. These include the Nicobar Islands (Bachman et al. 2022) and the western sides of islands in the Thai-Andaman Sea (Wall et al. 2015, Liu et al. 2022). Here, the rapidly fluctuating SSTs and SST depressions, associated with LAIW, which occur throughout the year, but are particularly prevalent during times of seasonally maximal SSTs (April–June), provide an environment where thermal stress is buffered and corals are less susceptible to bleaching (Wall et al. 2015, Schmidt et al. 2016). Similar benefits to reef corals afforded by internal waves have been described in the Coral Triangle of Southeast Asia (Storlazzi et al. 2020, Bachman et al. 2022), in the Galapagos and Pacific Shelf of Central America (Bachman et al. 2022) and in the South China Sea (Tkachenko & Soong 2017, Reid et al. 2019).

Physiological characteristics and thermal defences of corals

While the apparent resilience of coral reefs in the Andaman Sea can be attributed to the environmental conditions that surround them (e.g. the extreme physical habitat of inshore intertidal reefs and the temperature buffering effects of LAIW for offshore subtidal reefs), these environments have also resulted in the evolution of coral physiological characteristics that offer stress protection. Previous description of physiological attributes of corals from the Andaman Sea focused on densities and clades of coral symbiotic algae, as well as coral growth rates, behavioural responses and biochemical defences against stress (Brown 2007). Over the last 16 years, major advances have been made in molecular and genetic analyses of coral algal symbionts and their environmental tolerances (LaJeunesse et al. 2014, LaJeunesse 2017, Bellantuono et al. 2018, LaJeunesse et al. 2018), coral nutrition and the significance of heterotrophy at times of thermal stress (Rodrigues & Grotolli 2007, Houlbreque & Ferrier-Pages 2009) and the potential importance of coral microbial associations in stress protection (Ainsworth & Gates 2016, Ziegler et al. 2017, van Oppen & Blackall 2019).

While it is clear that the coral animal host can offer significant bleaching protection (Baird et al. 2009) with intertidal corals from the Andaman Sea showing a suite of host biochemical defences in response to temperature/light stresses (Brown et al. 2002), research has also postulated that specific coral symbiotic algae have thermo-tolerant traits, which offer the coral host partial protection during temperature-related bleaching events (Baker et al. 2004, Fabricius et al. 2004, Lien et al. 2007, Abrego et al. 2008, Jones et al. 2008, Stat & Gates 2011). The association of corals with one specific algal symbiont genus *Durusdinium* (previously Clade D) (LaJeunesse et al. 2014, 2018) is a case in point. A survey of the geographic distribution of different symbiont genera in corals from both inshore and offshore sites in the central Thai-Andaman Sea (LaJeunesse et al. 2010) revealed that the dominant genera were *Cladocopium* (formerly Clade C) and *Durusdinium* at both sites. Comparison with results from the western Indian Ocean and the Great Barrier Reef showed that *Durusdinium* was significantly more frequent among coral hosts collected from warm and turbid sites in the Andaman Sea than in the aforementioned locations, with corals displaying a prevalence and high diversity of *Durusdinium*, particularly in intertidal settings (LaJeunesse et al. 2010). The latter authors suggest that a combination of a high temperature environment and variable light conditions has facilitated the ecological radiation of *Durusdinium* in the Andaman Sea, factors which likely also explain the presence of this genus in corals from highly stressed reefs in Singapore (Tanzil et al. 2016, Poquita-Du et al. 2020). While the high thermal tolerance of symbionts from this genus is well established (Stat & Gates 2011, Guest et al. 2016, Bellantuono et al. 2018), recent genomic work also shows that the *Durusdinium* genome encodes for a cluster of genes involved in the synthesis of mycosporine amino acids, which offer photoprotection that reduces coral bleaching susceptibility (Shoguchi et al. 2018).

Another factor that limits damage to corals caused by elevated seawater temperatures is the ability of corals to survive prolonged bleaching events through heterotrophic nutrition (Grottoli et al. 2006, Baumann et al. 2014, Travaglione et al. 2023). Fine suspended particulate matter can be an important food source for corals living in turbid inshore waters (Anthony 1999, 2000). In such settings, bacteria, microbial exudates and adsorbed and detrital organic matter are present in the water column together with mucus sheets and strings sloughed off the coral surface after aerial exposure on intertidal reefs (Krupp 1984). Such mucus sheets have the potential to increase bacterial production in the water column (Taniguchi et al. 2014) and potentially contribute to a heterotrophic source of nutrition in specific corals (Houlbreque & Ferrier-Pages 2009). The turbid inshore waters of the Andaman Sea thus provide an ideal environment for heterotrophic feeding, and both branching and massive species in shallow waters around southeast Phuket have been observed ejecting mucus bound sediment boluses from the mouths of coral polyps following ingestion 2 hours after high tide (L. Putchim – personal communication). At this site, the organic content of suspended particulates is enhanced by macrophytes, which contribute up to 42% of sedimentary carbon (Tuntiprapas et al. 2019) and by mucus/fine sediment flocculants produced through mucus release by intertidal corals on flooding tides (Brown & Bythell 2005). The scope for heterotrophic feeding in corals is also enhanced on the sides of offshore islands subject to LAIW where high energy reserves observed in *Pocillopora meandrina* were ascribed to heterotrophic nutrition acting in combination with autotrophy (Roder et al. 2010).

An additional influence on coral thermal tolerance is the bacterial communities that they host (Gilbert et al. 2012, Ziegler et al. 2017, Gardner et al. 2019). Different bleaching susceptibilities among coral species are associated with distinct bacterial community profiles (Gardner et al. 2019), while the presence of coral associated nitrogen-fixing bacteria might benefit thermally stressed corals (van Oppen & Blackall 2019). In manipulative experiments, the bacterial community composition of corals appears to differ across thermally variable habitats, with the consortium being able to adapt to a new environment when corals were reciprocally transplanted (Ziegler et al. 2017). The dynamic nature of the coral bacterial community is well illustrated in recent work from the Thai-Andaman Sea where shifts in the composition of bacterial associates are associated with the age of the coral (Williams et al. 2015), changing tidal patterns (Sweet et al. 2017), elevated temperature experiments in the laboratory (Doering et al. 2021) and temperature-induced bleaching in the field (Pootakham et al. 2018, 2019, Chavanich et al. 2022). Interestingly, in a study of changes taking place in the coral *Porites lutea* pre, during and post the 2016 bleaching event, the coral bacterial community in corals from Ko Racha rapidly returned to their pre-bleaching state at least 3 months after the bleaching event, unlike those at the nearby island of Maiton where corals retained their bleaching state microbial consortium at this time (Pootakham et al. 2018). These differing responses might have been due to the influence of LAIW and the cooler temperature regime operating at Ko Racha, compared with Maiton, which is not affected by LAIW (Pootakham et al. 2018).

Possible limitations of coral resilience in the Andaman Sea

From the foregoing discussion, it is clear that the resilience of corals in the Andaman Sea spans from the cell to the ecosystem level, with ecological resilience being defined as the ability of a system to withstand disturbance without changing its overall identity in terms of structure and function (Nyström et al. 2001, Donovan et al. 2023). Coral reefs in the Andaman Sea have demonstrated some resilience in the face of repeated disturbances over the last 40 years unlike reefs elsewhere where disturbance has led to decreased hard coral cover and, particularly in the Western Atlantic, increases in macroalgae cover and a phase shift to algal-dominated communities (Hughes 1994, Mumby 2009, Tebbett et al. 2023). Factors contributing to such dramatic changes include increased nutrients, increased macroalgal cover and a decline in herbivory. While quantitative data on these parameters are limited for the Andaman Sea, published work (Phongsuwan & Chansang 1992, Souter et al. 2020b, Chan et al. 2023) and field observations suggest that macroalgal levels on coral

reefs are very low in the region generally being less than 3% (T. Wagh – personal communication, N. Phongsuwan – personal communication and A.H. Baird – personal communication). One reason for these observations is the reports of healthy herbivorous fish populations in the Thai Andaman Sea, the Andaman and Nicobar Islands (where they are not target species) and Pulau Weh in northern Sumatra (Campbell et al. 2012, Rangseethampanya 2022) (and U. Satapoomin – personal communication, T. Wagh – personal communication). In the Myeik Archipelago of Myanmar, fish biomass on reefs is reported as generally low because of local fishing pressures, but urchin populations are abundant and these act to limit algal growth (Howard 2018) with coral cover on these reefs being recorded as the highest in the Andaman Sea (Souter et al. 2020b).

Despite the potential resilience of subtidal and intertidal corals in the Thai-Andaman Sea and along the Myanmar coastline and the buffering effects of LAIW and rising sea levels on offshore reefs, there are obvious limitations to the tolerances of reef corals in the region. Examples of acclimatisation to rising sea temperatures in the Andaman Sea are scant though corals on intertidal reefs develop tolerances to high light intensities, which in turn provide decreased susceptibility to elevated temperatures (Brown et al. 2000, 2002). Such tolerances are retained for at least 10 years despite the removal of the initial triggering high light influence (Brown et al. 2015) though it is not known whether these responses are under epigenetic control nor if they are inheritable, as shown in *Platygyra daedalea* from the Arabian Peninsula (Liew et al. 2020), this species being a prominent member of intertidal coral communities in the Andaman Sea. Such factors are relevant when considering the effects of rising sea level on currently intertidal reefs, where the length and timing of aerial exposure would be reduced in future climate scenarios. Under such conditions, the initial ecological response of the coral community is increased coral cover as physical stresses are reduced and the environment becomes more benign (Brown et al. 2011, 2019, Dunne et al. 2021). The outstanding question must be, would intertidal corals of the Andaman Sea and other shallow, ponded habitats ultimately lose their superior high light and temperature tolerances over time as the climate warms and sea level rises?

The long-term temperature buffering effects of LAIW, such as those described in this paper for Andaman Sea corals, have also been questioned (Woodson 2018). Woodson proposes that warming seas will increase stratification, which will in turn require more energy input into internal wave formation, resulting in weaker, more stable waves that limit turbulent mixing and reduce the high variability in SSTs. Woodson also notes that sub-thermocline waters might become more hypoxic and acidic so that coral reefs, presently considered as thermal refuges through exposure to LAIW, become subject to additional environmental stresses. In this context, it is interesting that Schneider (2018) proposes that what might have been an appropriate refugium for initial conditions during the onset of a global climate crisis may ultimately turn into a trap as conditions deteriorate with the initial refugium no longer being adequate for survival. However, Schneider argues that potentially short-term refugia, such as the LAIW thermal refugia in the Andaman Sea, will be important in the early stages of perturbations caused by climate change even if they become inadequate later. Interestingly, in 2007, there was an occasion when upwelling from hypoxic and acidic sub-thermocline waters on offshore islets on the Thai mainland coast at Krabi, near Phuket, caused mass mortality of reef organisms and fish (N. Phongsuwan & S. Khokiattiwong – personal communications).

The projections of increasing frequency and the strength of ENSO (Cai et al. 2022) and *p*IOD (Nakamura et al. 2009, Abram et al. 2020, Cai et al. 2021) as climate warms will also provide challenges for Andaman Sea reefs with respect to increased sea temperature (ENSO) and periodic lowered sea levels (*p*IOD and ENSO). If there are repeated extreme SST events, such as that which caused the 2010 bleaching, on a regular basis (<5 years), then reef status would dramatically decline in the region since the recovery of subtidal and intertidal reefs from this event in the Thai-Andaman Sea has taken at least 12 and 8 years, respectively (Figures 10 and 11), together with significant community changes evident on some subtidal reefs. Furthermore, in 2010, the ENSO induced a delay in the onset of the wet monsoon, which normally would bring cloudy conditions and lowered SSTs to the region (Liu et al. 2022). The arrival of the wet monsoon would usually reduce sea temperatures,

but in 2010, the monsoon was delayed by 2 weeks and prolonged the duration of thermal stress, with Liu et al. (2022) suggesting that thermal refugia in the Andaman Sea could be threatened by such delayed monsoon onsets. Recent work on sediment cores from the Bay of Bengal (Wang et al. 2022) suggests that sustained warmer sea surface temperatures in the equatorial and tropical Indian Ocean during the Last Interglacial increased convective rainfall above the ocean but dampened Indian summer monsoon intensity on land. These findings contrast with other studies describing stronger monsoons during warm interglacial periods and highlight the need for better understanding of the controls on monsoon variability, factors which are important not only on land but also for the coral reefs of the Andaman Sea.

Another factor that is critical for coral reefs in the region is the growth of the dominant reef building coral *Porites lutea* and its ability to keep pace with rising sea level as the climate warms and bleaching events become more frequent (Perry et al. 2018). In a modelling study based in the Caribbean, it was shown that impacts on extension rates of two abundant corals (*Orbicella annularis* and *Porites astreoides*) had a synergistic negative impact on community resilience when compared with the effects of bleaching (Bozec & Mumby 2015). In the Thai Andaman Sea, recent studies of *Porites* growth rates at a limited number of sites around Phuket reveal that over a 30-year period (1980–2010) there has been a significant decrease in both linear extension (~20%) and calcification (~19%) of *Porites* (Tanzil et al. 2009, 2013), with linear extension falling dramatically by 27.6% in bleached corals and 7.2% in partially bleached corals between June 2010 and January 2011, following the extreme bleaching event of 2010 (Tanzil 2012). Rates of seawater warming in the Andaman Sea over the period 1980–2010 are almost twice those in the South China Sea, where decreases in calcification and linear extension at sites around the Thai Malaysia peninsula have been correlated with average annual sea temperature (Tanzil et al. 2013). These authors argue that it is likely that increasing SST is not the sole driver of reduced calcification in the region and that other factors such as river and stream run-off may also play a role. The Andaman Sea receives run-off from several rivers such as the Ayeyarwady (Irrawaddy), Thanlin (Salween), Sittang and Yangon in Myanmar, as well as drainage from streams and extensive mangrove forests on the west coast of Thailand and around the Andamans and Nicobars. While the Ayeyarwady has been ranked as one of top five rivers in the world in terms of its suspended sediment load (~326 Mt year⁻¹) (Robinson et al. 2007, Baronas et al. 2020), most of the suspended sediment is deposited in the Gulf of Martaban on the southern coast of Myanmar (Chen et al. 2020). The reefs of the Myeik Archipelago, much further south, are not directly affected by the sediments from the Ayeyarwady, but the northern reefs of the Myeik Archipelago will be influenced by the lowered salinity regime (31–33 psu) that results from the Irrawaddy River Jet, a freshwater jet discharged from the river that accumulates over the continental shelf of the Andaman Sea during the south west monsoon when strong south westerly winds prevail (Pargaonkar & Vinayachandran 2022). Recent work has also shown that the central Andaman Sea is also subject to reduced salinity effects, described as a ‘freshening’, with these events being correlated with strong pIODs (Liu et al. 2024). Such phenomena means that many reefs in the region are likely to be exposed to high spatio-temporal variations in physical and chemical parameters that might also impact coral calcification processes. Indeed, it has been proposed that future climate scenarios will see reefs affected by severe bleaching unable to maintain their vertical growth (Perry et al. 2018). Information on carbonate budgets for reefs in the region is limited to a single study on the intertidal reefs at Phuket, where Scoffin (1997) calculated a budget of 3 kg CaCO₃m⁻²year⁻¹ based on the calcium carbonate production of five dominant genera. This figure is considered relatively high both for the Indian Ocean (Perry et al. 2018) and for a reef flat setting, where calcification rates are often lower than on the shallow reef front (Saunders et al. 2015). However, it should be noted that the carbonate budget study was carried out over 25 years ago, well before the extreme bleaching of 2010 and successive bleaching events, though recent studies in the Chagos Archipelago in the central Indian Ocean (Lange et al. 2022) indicate that carbonate budgets here showed some recovery 6 years after a major bleaching event in 2015–2016.

Rising SSTs are already having an impact on the reefs of the Andaman Sea, and while select sites have the ability to recover relatively rapidly from severe bleaching events, future climate scenarios potentially pose much more serious threats to corals currently living in thermal refugia and those in shallow, turbid inshore sites.

Conclusions

This review has relied predominantly on recent work carried out on coral reefs and related oceanography in the Thai-Andaman Sea since research in other countries bordering the area has been mainly restricted to ecological surveillance of coral reefs. There are, however, common patterns to be discerned in reef survey results across the region, the most obvious being the susceptibility of corals to the extreme temperature-induced bleaching of 2010. Corals throughout the Andaman Sea suffered a high mortality in response to this bleaching event with over 50% loss of coral cover at many sites.

Another common regional pattern is the gradual recovery of reefs since 2010. The recovery of coral cover at monitored intertidal and subtidal reefs throughout the region has taken ~8–12 years, with some interruption of recovery because of a less stressful temperature-induced bleaching event in 2016 (subtidal and intertidal corals) and lowered sea-level and elevated SSTs (intertidal corals) in 2019. Since 2010, an upward trajectory in coral cover at monitored sites is evident, with the most recent surveys in the Thai-Andaman Sea showing coral cover values approaching those of the late 1990s, though changes in coral species dominance have also been noted at some locations.

Despite a susceptibility to extreme bleaching events, corals in the Andaman Sea display some resilience to rising sea temperatures. The basis of such resilience is found in selected environments such as westerly facing reefs subject to highly fluctuating SSTs because of exposure to LAIW, turbid inshore settings and intertidal habitats, where corals have developed physiological adaptations to survive physical conditions operating at these locations.

Global assessments of reefs portray the Andaman Sea as an area where coral cover is not in decline, and several publications highlight the above habitats as potential refugia for corals. These views, however, must be tempered by the fact that reefs in the Andaman Sea are also affected by increasing anthropogenic influences (other than climate change), and future climatic scenarios project not only a background increase in SST but also an increasing incidence and frequency of ENSO and *p*IOD events, combined with potential modification of internal wave regimes and rising sea levels, which would not, in the long-term, necessarily be favourable to all the reefs in the region and which could undermine any observed resilience. It is already evident that coral calcification rates in the region have significantly declined in recent years, a result that is correlated with rising SSTs. Studies on the Great Barrier Reef have also shown that climate refugia fail to protect reefs when global warming exceeds 3°C, a climate scenario that is now predicted by 2100 (McWhorter et al. 2022). In addition, Walsworth et al. (2019), using modelling simulations, suggested that protection of habitat heterogeneity and connectivity provided greater long-term conservation benefits than implementing refugia strategies.

An improved understanding of the future of coral reefs in the Andaman Sea would be facilitated by a greater regional co-operation in maintaining regular reef monitoring using standardised protocols that ultimately extend coral cover measurements to coral community structure changes and demography of dominant coral species. The current taxonomic framework for the Scleractinia is, however, a significant impediment to population level studies in the Indo-Pacific (Kitahara et al. 2016, Cowman et al. 2020, Bonito et al. 2021, Bridge et al. 2023). Alongside reef monitoring, long-term *in situ* observation of seawater parameters, especially those related to anthropogenic inputs (e.g. nutrients, sediments and emerging pollutants), would aid in interpretation of responses of coastal reefs to chronic stressors. The region would also greatly benefit from an expansion of existing coral reproduction/gene flow studies (Chanmethakul 2002, Chanmethakul et al. 2023, Fiesinger et al. 2023) and interdisciplinary collaboration between biologists, oceanographers and modellers to identify connectivity corridors and patterns of larval dispersal, which might enhance

or, if dispersal was limited, limit coral resilience (Mizerek et al. 2021). McManus et al. (2021) consider that maintaining evolutionary potential and habitat connectivity are both vital for the continued existence of coral reefs. Only with greater regional co-operation and international collaboration will it be possible to assess more accurately the true resilience potential of corals in the Andaman Sea and the conservation practices needed to protect them.

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