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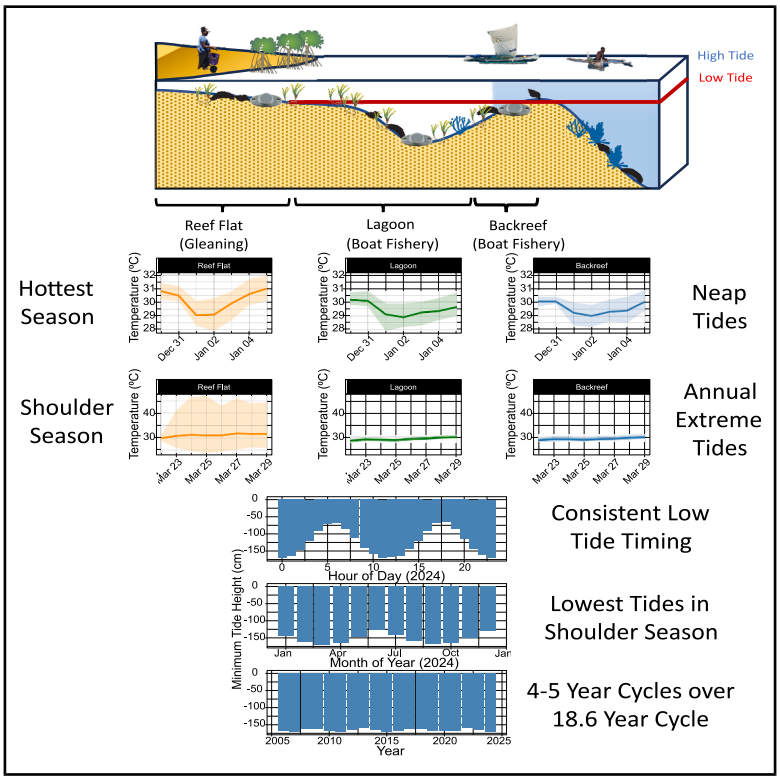
# Asymmetric thermal risks across Malagasy macrotidal reef zones threaten socioeconomic outcomes for local fisheries

## Graphical abstract




## Highlights

- The thermal exposure of Malagasy fisheries depends on tide, season, and gear
- The intertidal reef flat experienced thermal extremes out of sync from summer
- Annual tide height cycles drive thermal stress and fishing access
- Sea cucumber harvest concentrates in the reef's most thermally extreme zones

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## In brief

Villeneuve et al. show that small-scale fishers in Madagascar face different climate risks depending on how and where they fish. Reef habitats used by gleaners reach extreme temperatures at different times of year than deeper zones used by boat-based fishers, exposing gleaned species to heat stress that current fishery management does not yet account for.

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# Asymmetric thermal risks across Malagasy macrotidal reef zones threaten socioeconomic outcomes for local fisheries

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**SCIENCE FOR SOCIETY** Artisanal fisheries across the Western Indian Ocean coral reef systems are a critical source of nutrition and income for coastal communities. Boat-based fishing is a dominant fishery method in deeper parts of the reef, but many of the poorest and most marginalized fishers, especially women, depend on gleaning (fishing on foot) in shallow, exposed reef habitats. As ocean and air temperatures rise, we know remarkably little about how heat exposure differs across these habitats and, thus, how climate change will affect the different fisheries that depend on them. We spent over a year measuring temperatures across reef habitat zones on a Malagasy reef where both gleaning and boat-based fishing occur, paired with fishery catch records from the same reef. Gleaning habitats on the intertidal reef flat reached temperatures as high as 48.8°C. Counterintuitively, these extremes did not coincide with the hottest months of the year. Instead, the reef flat is hottest during shoulder seasons, when the year's lowest tides happen to fall during the heat of the day. Gleaned species, including economically important sea cucumbers, therefore face their greatest thermal risk on a different calendar than boat-based fishers working deeper reef zones.

These findings have direct implications for climate-adaptive fishery management. Marine protected areas in the region, including the one governing our study site, do not currently distinguish between the reef zones used by gleaners versus those used by boat-based fishers, nor do they account for different seasonal heat exposure. Effective management in a hotter climate future should consider timing monitoring and support programs to target seasons of the highest heat risk, protecting gleaners' access to productive but thermally vulnerable habitats and helping diversify livelihoods.

## SUMMARY

Fishery management and climate adaptation in the coastal zone often overlook how marine microclimates vary through space. In tropical macrotidal systems, gleaning fisheries are an important source of nutrition among local communities and are restricted to intertidal habitats. Here, we report habitat temperature across subtidal and intertidal reef zones in southwest Madagascar using over a year of *in situ* temperature data and decadal tide cycle analysis, contextualized with fishery catch and species composition data. Temperatures on the intertidal reef flat reach 48.8°C, with peak heat occurring during shoulder seasons rather than peak summer, driven by midday low tides. Fishery data reveal that shallow, warm areas of the reef provide substantial biomass, effort, and much of the region's sea cucumber catch. Gleaning habitats experience thermal extremes that are both more intense and seasonally offset from subtidal boat-fishing zones, an important consideration for climate-adaptive management of spatially segregated and economically sensitive fisheries.

## INTRODUCTION

Chronic ocean warming and acute heatwaves are predicted to increase water temperatures within reef systems, particularly in the Western Indian Ocean (WIO).[1–4] Distinct thermal microclimates may arise across reef zones due to complex interactions between bathymetry and water movements in the nearshore zone of coastal reefs, leading to coastal reef zones experiencing climate change differently from the open ocean. Since human activity is concentrated in these coastal zones, understanding the current and future microclimatic trends of reefs can improve conservation and management decision-making.[5] Coastal socioeconomic systems in the WIO are strongly linked to the ecological functioning of marine ecosystems and are thus predicted to be at a higher risk of disruption compared with areas of more rapid warming in developed countries.[6–8]

Within the WIO, southwestern Madagascar is particularly vulnerable to the social and ecological impacts of climate change and heatwaves. Reefs provide critical fisheries and ecosystem services for people in nearby cities and villages, where livelihoods and income are highly dependent on the reef function.[6,9–12] Compound stressors encompassing climate change, fishery pressure, decreasing water quality, cyclone activity, changing land-use patterns, and increasing populations due to coastal migration have placed profound stress on these reefs.[13–15] While much of the conservation focus on the fringing reef system of southwestern Madagascar has been on unsustainable harvest and adherence to marine protected area (MPA) policies, there has been relatively little work examining the sensitivity of this marine system to climate change. Nonetheless, these reefs experience recurrent thermal stress,[16–18] which contributed to historic wide-scale coral bleaching in 1998 and 2016.[18,19]

Assessments of reef temperatures in southwestern Madagascar have almost exclusively been made using remote-sensed data products,[3,10] which mask the information from coastal reef ecosystems in which most artisanal fisheries operate. Internal waves, water mass pooling, and other hydrodynamic phenomena can result in subtidal heterogeneity on reef systems, further complicating assessments of thermal stress on complex coastal reef systems.[5,20–23] Reef flat and shallow lagoon environments are expected to experience higher average and maximum temperatures than deeper zones, as the latter experience mixing of cooler offshore waters from greater depths with warmed shallow waters.[20,23,24] Complicating any assessment of thermal stress experienced by fished species is the interaction of the macrotidal semidiurnal tide system in southwestern Madagascar, with a tidal range of around three meters.[25,26] When these habitats are exposed to the ambient air, air temperatures are not a reliable proxy for the body temperatures of fished organisms due to interactions between organisms and the physical environment, which can change with time. Tidal emersion on reefs, when timed with solar exposure, can result in coral bleaching and mass mortality in reef invertebrates, including fished species such as sea cucumbers.[27–33] While coral bleaching has been recorded in response to thermal stress in southwestern Madagascar,[6,10,18,34–36] the impacts of these heatwave events on fished species are understudied.

In addition to national and multinational industrial fishing, a large proportion of fisheries in the WIO are artisanal (catches sold at the market) and subsistence (catches consumed at home) and provide much of the coastal population's nutrition and livelihoods.[8,37] In meso- and macrotidal areas of the WIO, men and women tend to fish in different habitats using distinct gear, with men typically using boats to access offshore sites and employing nets and lines.[38] Women, by contrast, fish on foot in nearshore areas, harvesting benthic invertebrates with hand-held tools.[39–42] This type of fishing by foot, or gleaning, is the predominant fishing method for women and low-income households.[40,42,43] Gleaning (fishing on foot, often with hand spears) tends to be restricted to coastal areas accessible by foot, such as mangroves, intertidal flats, seagrass beds, and reef crests, and occurs primarily during calmer seasons.[44–48] Fishers with fewer economic resources often practice gleaning, which does not require a boat or substantial capital investment. While some species like octopus can be found in both deep and shallow habitats, the species composition and abundance within catches vary dramatically between habitats and fishing type.[40,49–51] For example, sea cucumbers are predominately caught and farmed in shallow lagoon and reef flat zones for the export market and are less present from catches in deeper waters.[52,53] Fished species that are restricted to shallow reef zones, like sea cucumbers, may be at elevated risk for physiological stress during extreme marine and atmospheric heatwave conditions.

Given the asymmetric impact of climate change and heatwaves (both marine and atmospheric) on shallow-water coastal ecosystems, it is possible that species and habitats targeted by women and the least wealthy of a given fishing community will be impacted first and to a greater magnitude than boat-based fisheries dominated by men in deeper waters. Gleaning and fishing in shallow reef zones disproportionately provides nutrients to the local food supply,[54–56] and it is likely that disturbances affecting gleaning catches will have a direct impact on coastal food security. Further, if climate change, drought, and overfishing lead to abandonment of boat-based fisheries and inland agriculture, gleaning pressures may increase on coastal habitats as people seek alternative sources of livelihood and food.[57]

Here, we describe the thermal environment of Salary Reef, southwestern Madagascar, across four reef geomorphic zones (backreef, shallow and deep lagoon, and reef flat) that encompass subtidal and intertidal sites by deploying long-term temperature loggers (Figures 1, S1, and S2). We further model the 18.6-year tidal cycle[58] of Salary Reef to assess reef flat immersion timing on a yearly, seasonal, and daily basis. We contextualize our analysis of the physical environment with fisheries-dependent catch and species composition data from fishers based in Salary village, showing the importance of shallow reef habitats for fisheries. In particular, we focus on biomass and catch-per-unit-effort (CPUE) of sea cucumbers. We show that assumptions of equal extreme heat events in space and time risk missing critical subsistence fisheries vulnerabilities to climate change.

## RESULTS

### Reef microclimate variability

Of the three subtidal data loggers (shallow lagoon, backreef, and deep lagoon; $n$ = 43,422, 44,208, and 34,500 observations

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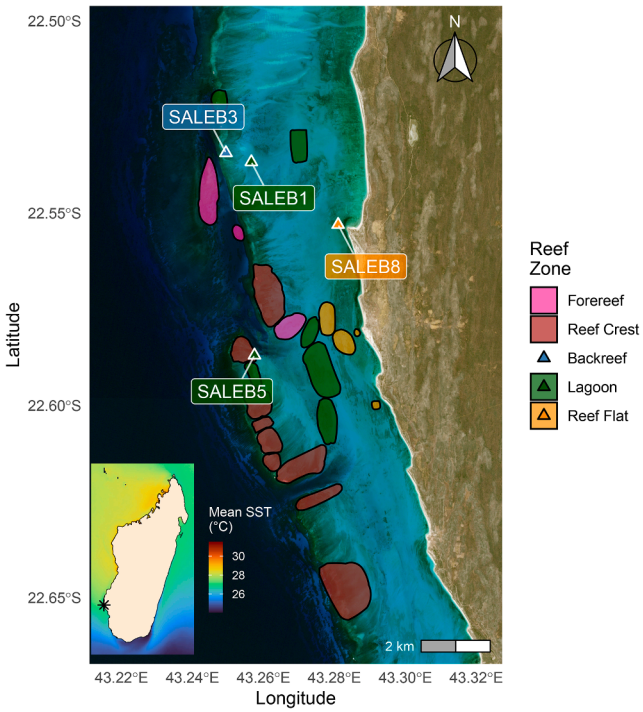


**Figure 1. Temperature logger deployments across named fishing areas and geomorphic zones on Salary Reef**

Colored triangles show recovered logger locations with their corresponding reef geomorphic zone, and the locations of fishing sites are indicated with polygons. Of the nine deployed loggers on the reef, we recovered four loggers (shown) across three of the reef's geomorphic zones. The location of the air temperature logger is not shown. Recovered loggers did not span all reef zones, and not every named fisheries site is represented on the map. Original satellite imagery is from Copernicus Sentinel 2, July 2023, retrieved from Copernicus Browser (https://browser.dataspace.copernicus.eu) and licensed under CC BY 4.0. The inset map depicts the location of Salary Reef within Madagascar with accompanying mean yearly sea surface temperatures (2010–2020, Bio-ORACLE).[59]

See also Figures S1 and S2 and Table 1.

[obs/15 min]), the backreef site (SALEB3) had the highest overall mean (27.3°C) and maximum (33.4°C) temperatures (Figure 2). The backreef also spent a similar number of hours (1,446 h) above the Coral Reef Watch (CRW) bleaching threshold of 30°C (Southwestern Madagascar Coral Reef Watch threshold[60]) as the shallow lagoon site (1,478 h, Table 1). The deep lagoon site (SALEB5), the deepest site overall, had the lowest mean (27.08°C) and maximum temperatures (33.0°C) and the fewest number of hours (1,089.2 h) above the CRW 30°C threshold. A Kruskal-Wallis test confirmed that water temperature was significantly different between sites ($H_2$ = 160.5, $p < 0.0001$). Post hoc multiple comparisons indicated significant differences between all sites, although the significance between the two shallow sites (SALEB1 and SALEB3) was weak (Bonferroni-adjusted multiple comparison, $p = 0.0452$, Table S3), while the deep lagoon site was significantly cooler than both shallower sites ($p < 0.0001$ Table S3).

We further calculated the daily variance and temperature range of each subtidal logger; only the temperature range was significantly different between sites (daily range Kruskal-Wallis, $H_2$ = 16.7, $p$ = 0.0002). The daily temperature range was highest at the backreef site (SALEB3) and lowest at the shallow lagoon site (Table 1). Post hoc comparisons demonstrated that the temperature range at the backreef site was only significantly different from the shallow lagoon site (SALEB1, $p = 0.0001$, Table S4). Despite having a mean temperature of only 0.18°C/0.21°C below the shallow lagoon and backreef sites (respectively) and a maximum temperature of only 0.1°C/0.4°C less (shallow lagoon/backreef), the deep lagoon site had 26%/24% fewer hours above 30°C compared with these sites (shallow lagoon/backreef).

The seawater temperatures measured *in situ*, summarized as daily means, and those measured from reanalysis products (optimal interpolated sea surface temperature [OISST], Copernicus) were not significantly different, indicating that variability driving site-level differences occurs on a sub-daily timescale (Kruskal-Wallis test, $H_4 = 4.46$, $p = 0.347$, Figure S3). Correlation ranged between 0.86–0.96 ($R^2$, reef flat and shallow lagoon) for water logger data and Copernicus data, and between 0.76–0.92 ($R^2$, reef flat and deep lagoon) for logger data and OISST data (Figure S5). However, OISST tended to underpredict the hottest values observed with loggers, while the Copernicus dataset at a 0.5 m depth better matched the distribution of observed data (Table S2; Figure S3). Correlations between each 15-min logger observation and daily reanalysis data were lower than the summarized logger data values, with correlations ranging from 0.62–0.93 ($R^2$, reef flat and backreef) for water logger data and Copernicus data and between 0.54–0.89 ($R^2$, reef flat and deep lagoon) for water logger data and OISST data (Figure S6).

The intertidal temperatures collected at SALEB8 (reef flat) were different from the other subtidal temperature series due to periods of air exposure during low tide ($n$ = 34,211 observations [obs/15 min]). Both exposure during low tide and the day/night cycles modulated the temperatures experienced at this site, as indicated by strong wavelet power levels associated with 8-h (length of submersion), 12.4-h (diel tidal cycle), and 24-h (daily cycle) cycle periods (Figure 3). We observed minor significance in 2-week periods, potentially due to tidal flushing or upwelling events.[25] Vertical bands below the 12.4-h periods correspond to a combination of tidal harmonics and variable emersion durations under seasonally changing tidal amplification. The average emersion duration was 2.36 h (median 2.47 h), although the left-skew of tidal emersion duration indicates longer durations, up to 3.7 h, are more frequent (Figure S9). The three other subtidal loggers showed power bands over the 12.4- and 24-h wavelet periods, again indicating the influence of tidal and solar cycles on temperature regimes on the subtidal reef (Figure S10). Finally, the air temperature recorded by the temperature logger displayed a strong 24-h wavelet period power band, corresponding with solar cycles, but also a seasonally moderate 12-h power band corresponding to atmospheric tides and land-sea breezes that are stronger during the cloudless warm-dry season (Figure S10).

The intertidal temperature data showed a strong seasonal pattern; we recorded extreme temperatures not in the peak wet season (January) but between March and June, and from August to October. Loggers recorded a maximum temperature

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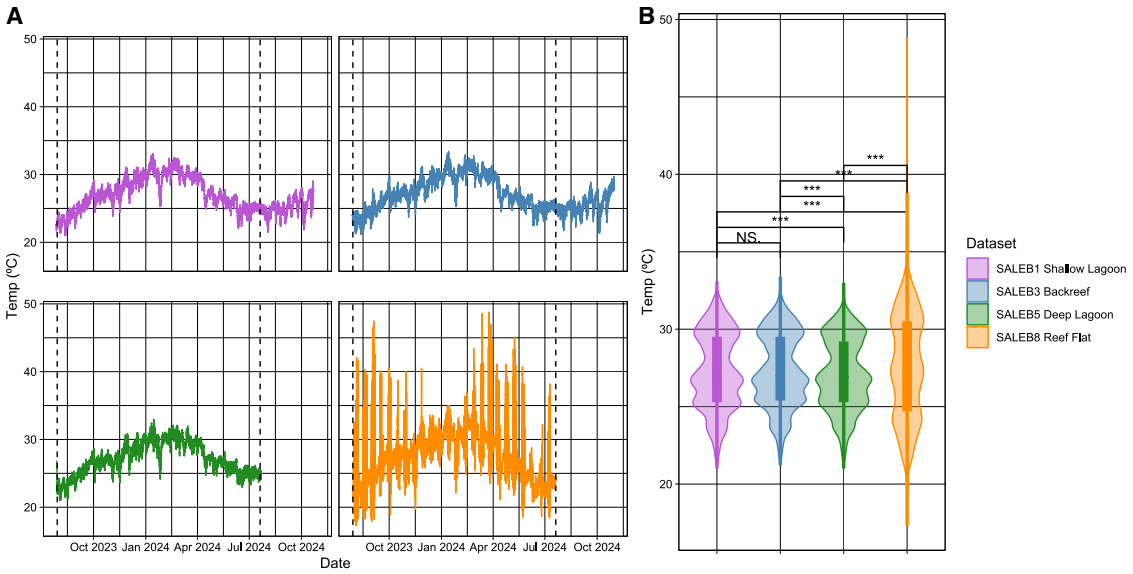


**Figure 2. *In situ* temperatures on Salary Reef observed over a year across four loggers**

(A) Temperature time series from the four recovered loggers on Salary Reef, SW Madagascar, are shown. Vertical dashed lines indicate the extent of data used for site comparisons. Data were collected every 15 min ($n$ = 43,422, 44,208, 34,500, and 34,211 for shallow lagoon, backreef, deep lagoon, and reef flat sites, respectively).

(B) The distribution of temperatures at each site is shown ($n$ = 34,272 observations/site in date-restricted dataset). Boxplots indicate mean and interquartile range (25%–75%). Asterisks give multiple comparisons (Wilcox's) significance across all loggers—note that in the text, we restrict our multiple comparisons to subtidal sites only, and therefore, there are slight differences in significance level.

of 48.8°C on March 24, 2024, with additional excessive heat days occurring on March 12, 2024 (48.6°C) and September 3, 2024 (47.5°C). Between November and February, water temperatures were consistently warmer than the air temperature in the intertidal zone, despite this being the hottest portion of the year in southwest Madagascar. These extreme temperatures can be attributed to low-tide events (Figure 4A). Examining the residuals of the relationship between the intertidal (SALEB8) and lagoon (SALEB5) loggers (linear model, $R^2$ = 0.64, $p < 0.0001$) reveals minimal variation from residuals of zero in submerged observations (Figure 4B). However, exposed observation residuals alternate between much warmer (~5°C–20°C, March–October) and cooler (~−5°C, November–February) than the water temperature in the lagoon. In short, low-tide temperatures were lower than other parts of the year, and indeed lower than the water temperature, during the hottest part of the year (wet season, November–March). Water temperatures were not significantly different between night and day observations (Figure 4C).

Residuals of the relationship between observations of the intertidal logger (SALEB8) and the air temperature (SALEB10) (linear model, $R^2$ = 0.44, $p < 0.0001$) show that low-tide logger temperatures were much warmer than air temperature, indicating the importance of additional factors (e.g., albedo and radiative forcing) on low-tide temperature on intertidal flats (Figure 4D). During the hot, wet season, the intertidal flat logger experienced fewer positive residual spikes with low tide while periodically having negative residuals. However, during the warm, dry season, flat logger temperatures routinely exceed air temperatures. The most extreme negative residuals were recorded during the daytime (Figure 4E). Mean hourly air temperatures recorded using temperature loggers generally matched those from ERA5 microclimate downscaling data ($R^2$ = 0.86, Figure S4)

## Decadal tide patterns

Tides during the field season of 2023–2024 occurred during a weakening in the 18.6-year lunar cycle—tides were less extreme (maximum amplitude of 3.4 m) than at the peak of the cycle in 2015–2016, particularly in the early warm-dry (May–July) and early hot-wet seasons (November–January; Figures 5 and S7). Early warm-dry season low tides spend more time below −1 m and have lower overall tides during the day than the night, while the inverse is true during early hot-wet period low tides, where nighttime low tides are generally longer and larger. In the late hot-wet and warm-dry months, there is no trend in monthly hours below −1 m or monthly minimum tide across years, indicating that the timing of extreme low tides is consistent along the 18.6-year tidal cycle. Tidal heights that exceed −1 m (and would therefore expose the intertidal flats logger) routinely occur between 09:00 and 15:00 (local time) across the 18.6-year tidal cycle, encapsulating solar noon (Figure S8).

## Spatial patterns in fishery catches

Across 1,442 fishing trips on Salary Reef, fishers harvested 7,739 kg of biomass during the study period. Fishing effort was highest in reef crest habitats, which accounted for 714 recorded fishing trips and 3,379.2 kg of catch biomass (Table 2). Lagoon and forereef habitats also supported substantial fishing activity (370 and 293 trips, respectively), whereas nearshore (includes

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**Table 1. Summary statistics of temperatures recorded on Salary Reef**

| ID | Zone | Fishing zone | Mean (°C) ± SD | Minimum (°C) | Maximum (°C) | Hours above 30°C | Daily range (°C) ± SD |
|---|---|---|---|---|---|---|---|
| SALEB1 | shallow lagoon | boat/subtidal | 27.26 ± 2.43 | 21.0 | 33.1 | 1,478 | 1.49 ± 0.48 |
| SALEB3 | backreef | boat/subtidal | 27.29 ± 2.33 | 21.2 | 33.4 | 1,446 | 1.7 ± 0.63 |
| SALEB5 | deep lagoon | boat/subtidal | 27.08 ± 2.26 | 21.0 | 33.0 | 1,089 | 1.58 ± 0.57 |
| SALEB8 | reef flat | gleaning/intertidal | 27.64 ± 3.57 | 17.3 | 48.8 | 2,510 | 6.42 ± 6.42 |
| SALEB10 | air temperature | N/A | 26.36 ± 4.6 | 12.3 | * | 1,917 | 11.45 ± 2.81 |

*In situ* temperatures are calculated between 2023-07-29 and 2024-07-20. Asterisk (*) denotes maximum air temperature values that were not calculated due to a short period of logger exposure to direct sunlight.

reef flat) and backreef habitats were used less frequently. Mean catch biomass per trip varied among geomorphic zones, ranging from 4.1 kg trip$^{-1}$ in the backreef to 7.0 kg trip$^{-1}$ in the nearshore habitats. Total catch and CPUE differed significantly across reef zones (Kruskal-Wallis, catch: $H_4 = 39.5$, $p < 0.0001$; CPUE: $H_4 = 28.1$, $p < 0.0001$; Table S6). This pattern was driven by forereef trips, which had significantly lower catch and CPUE than lagoon and reef crest trips (Dunn's post hoc, Bonferroni-adjusted, all $p < 0.001$) and lower catch than nearshore trips ($p = 0.0026$). No other pairwise zone comparisons were significant (Table S6).

Catch composition varied among geomorphic zones (Figure 6). Fish and octopus dominated catches across most habitats, together accounting for approximately 90% of total catch biomass in backreef and forereef habitats and approximately 85% in reef crest habitats. Lagoon catches were dominated by fish (52.6% of biomass), with contributions from octopus (17.6%), sea cucumbers (15.5%), and rays (11.4%). Backreef catches were dominated by fish (54.6%) and octopus (42.3%), while forereef catches were similarly distributed between fish (50.9%) and octopus (43.2%). Reef crest catches were composed primarily of octopus (43.1%) and fish (41.5%), with rays contributing 12.3% of biomass. Nearshore catches, which include reef flats, were dominated by fish (70.2%), with smaller contributions from octopus (17.6%) and sea cucumbers (11.0%).

Sea cucumber harvests were unevenly distributed among geomorphic zones (Table S5). Lagoon habitats accounted for the majority of recorded sea cucumber biomass (341.7 kg; 78.0% of total sea cucumber harvest), followed by forereef (37.8 kg), nearshore (34.7 kg), and reef crest habitats (24.2 kg), while no sea cucumber harvests were recorded in the backreef. Sea cucumbers were recorded in 124 lagoon fishing trips and 22 nearshore fishing trips; however, the proportion of trips containing sea cucumbers was highest in nearshore habitats, where sea cucumbers were present in 48.9% of monitored trips. Mean sea cucumber CPUE was highest in lagoon (0.71 kg fisher$^{-1}$ h$^{-1}$) and nearshore habitats (0.62 kg fisher$^{-1}$ h$^{-1}$).

## DISCUSSION

### Reef temperature regimes depend on reef zone and tide cycles

Through our analysis of *in situ* temperature data and long-term tidal amplification, we uncovered heterogeneity and extremity across four geomorphic zones within a barrier reef system in southwestern Madagascar. While the three subtidal sites had superficially similar thermal regimes and we could not achieve true spatial replication due to logger loss (see methods), we observed significant variation in the occurrence of extreme heat between sites. This agrees with other observations of small-scale reef variability across shallow and deeper reef sites elsewhere.[61,62] Many of the extreme subtidal observations (both maxima and minima) were larger than those obtained from two remote-sensed products, indicating that *in situ* logger observations describe the thermal environment with more fidelity. This is a common observation in reef systems, as remote-sensed and reanalysis products often mask coastal areas, spatially average, and do not account for microclimatic processes such as substrate albedo and water residence time.[63–66] Interestingly, the subtidal sites at Salary Reef all had larger temperature maxima and minima than reported from the nearby Grand Récif de Toliara (GRT).[67,68] Temperature variation between January and May at the GRT was much higher than at other times of the year at the same site, including the (on average) cooler months of July and August. We hypothesize this could be due to the influence of larger tides (observed in our study), increased cyclone activity, and internal waves arising from increased wind activity during this period.[66,67,69]

While all subtidal loggers presented an expected trend pattern of highest annual maximum temperatures during the hot-wet season (January–February), temperatures recorded from the intertidal flat logger displayed a contrasting pattern of elevated temperatures during the shoulder seasons. Air temperatures are not a reliable indicator of experienced conditions on the reef flat, as peak air temperatures did not align with the seasonality of peak intertidal temperatures. Rather, the dominant tide regime played a larger role in determining when extreme heat was experienced. While our intertidal temperature observations aligned with modeled tide timing on Salary Reef, it should be noted that intertidal exposure predicted from tide models will generally be inferior to *in situ* water pressure loggers in hydrodynamically complex macrotidal reef systems, much as remote-sensed sea temperatures fail to accurately describe fine-scale temperature regimes. Future work describing thermal environments on macrotidal must therefore account for local hydrodynamics.

Given chronic warming and acute heatwave events, we predict that the next ~16 years will see intertidal habitats in southwestern Madagascar experiencing hotter conditions than we observed during our deployment period. Our data was collected

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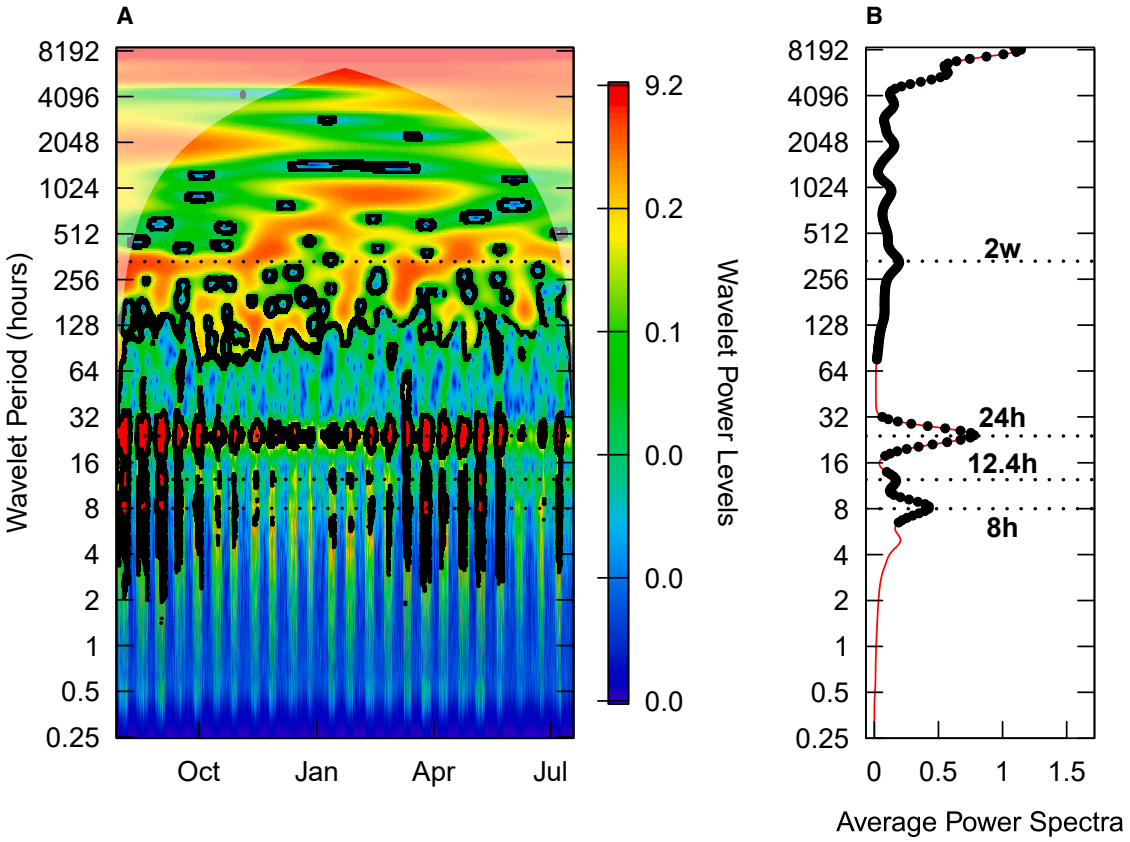


**Figure 3. Intertidal temperatures on Salary Reef are associated with tidal and diel solar cycles**

(A) Wavelet analysis of intertidal reef flat (SALEB8) temperature periodicity between August 2023 and July 2024. Black outlined areas indicate regions that have strong wavelet power support ($p < 0.01$). See Note S2 for wavelet methodological and interpretation details.

(B) Average power spectra illustrate the strongest periods observed over the logger deployment period. Black dots correspond to periods that were strongly statistically significant ($p < 0.01$).

See also Figure S10.

during a relatively weak tide period of the 18.6-year cycle, suggesting that intertidal temperatures in 2033 will reflect hotter, lower, and longer low-tide periods. This is critical because the two lowest tide windows between February and April and August to October are the most optimal for gleaning, both from a consideration of access to low tidal elevation seafloor and because of the relatively calm seas in this period.[45,53,69] Between these tide windows in the warm-dry season, wind speeds off southwestern Madagascar increase, which limits the number of days fishermen can access offshore sites and, for gleaners, the exposed offshore reef crest.[68,69] Furthermore, the stationarity of midday low tides throughout the year is a particular risk factor for tropical reefs in southwestern Madagascar. On the Australian Great Barrier Reef, the time forms of the tidal harmonics result in shifting low-tide timing over the year, such that extreme low tides occur only around midday in the winter, potentially offering thermal refuge to intertidal organisms.[29]

## Shallow reef zones are critical for fisheries

Reef crest habitats supported the greatest fishing effort and total catch biomass, while lagoon and forereef habitats also supported substantial fishing activity. In contrast, nearshore habitats accounted for relatively few monitored trips but exhibited the highest overall CPUE, indicating that these shallow habitats can provide productive fishing opportunities despite comparatively lower total fishing effort. Boat-based fishing on the forereef zone, exposed to the open ocean, was less productive than fishing in shallower, thermally variable habitats. Sea cucumber harvesting was concentrated within shallow lagoon and nearshore environments rather than being distributed evenly across the reef system. Differences in harvest among reef zones likely reflect a combination of habitat-specific resource distributions, fisher accessibility, market demand, and harvesting practices, although the importance of these factors cannot be measured from fisheries-dependent data alone.

Importantly, these fishery data represent harvested catch rather than direct measures of ecological abundance or standing stock. Therefore, the observed spatial patterns should be interpreted as evidence of the distribution of fishing activity and fishery productivity rather than direct estimates of resource abundance. In addition, some benthic invertebrate catches, such as sea cucumbers, may be underrepresented in the dataset given

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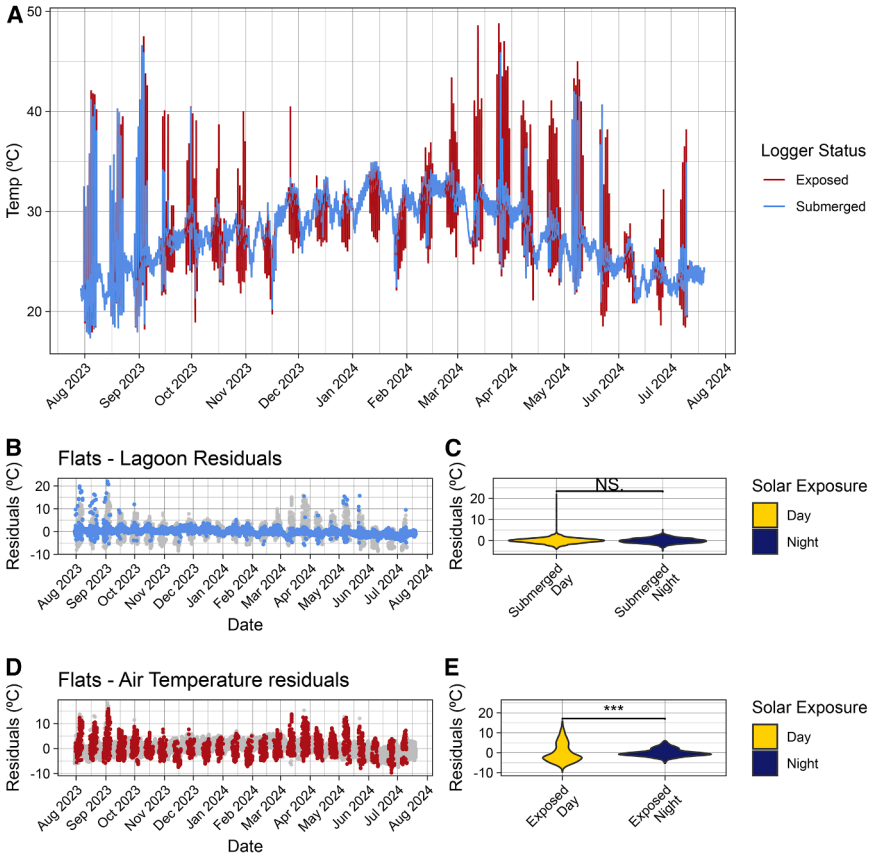


**Figure 4. Intertidal thermal extremes on Salary Reef occur in shoulder seasons, aligned with daytime low tides**

(A) Tidal exposure status of the intertidal flat (SALEB8) logger. Air exposure/water submersion status was determined via the application of interpolated logger tide height and offset from tidal model predictions. Logger status predictions in August and September 2023 erroneously identified heat spikes more often associated with low tide as submergence events. Temperature residuals from the lagoon (B and C, SALEB5, $n$ = 15,064 days, 14,772 nights [obs/15 min]) and air temperature residuals (D and E, SALEB10, $n$ = 1,832 days, 1,805 nights [obs/min]) from intertidal zone temperatures (SALEB8) are also shown.

See also Figures S7 and S8 and Note S1 for methodological details.

not every fisher could be interviewed, especially gleaners. The recorded contribution of sea cucumbers and other benthic invertebrates should therefore be considered a conservative estimate of their importance within the fishery, particularly in nearshore and lagoon habitats.

Nevertheless, these findings are particularly relevant in the context of the thermal analyses presented here because the shallow habitats most associated with sea cucumber harvesting were identified as among the most environmentally variable and thermally exposed components of the reef system. Previous studies from southwestern Madagascar indicate that women play an important role in harvesting benthic invertebrates from these shallow habitats.[38,39,41] More broadly, women's fisheries are frequently underrepresented in conventional monitoring and national fisheries statistics.[70–72] Environmental changes affecting thermally-stressed habitats may therefore have disproportionate consequences for invertebrate fisheries and the coastal communities that depend upon them.

## Inferring fishery climate resilience from reef microclimates

The fishery data presented here underscores the importance of measuring habitat heterogeneity across reef zones. We identified the intertidal reef flat and shallow lagoon reef zones as the most thermally variable and extreme, while also being the zones most critical for total catch biomass and sea cucumber harvest, respectively. While the fishery data did not discriminate between boat fisheries and gleaners, these patterns suggest that the species and habitats at greatest thermal risk are centrally important to local fisheries.

Elevated temperatures affect gleaned organisms both directly by altering physiology and behavior and indirectly through habitat degradation. The direct effects of thermal stress, mortality, and behavioral shifts in habitat use are most relevant to intertidal, shallow lagoon, and reef crest species that experience emersion or prolonged exposure to elevated water temperatures. Sufficient heat and air exposure during macrotidal low tides can cause mass mortality across reef invertebrate taxa, including holothurians, gastropods, and bivalves, as well as seagrass beds.[28–30,32,73–76] Indirect effects include the loss of structural coral and seagrass habitat, which provides nursery grounds and refuge for both fish and benthic macroinvertebrates.[77–80] While some intertidal coral colonies show elevated plasticity to aerial exposure during extreme tides,[32,81] this tolerance has limits.[82] Before 1978, extensive coral cover of the reef flat by branching *Acropora* was reported from the GRT, approximately 100 km south of Salary.[68] By 2008, this intertidal coral cover was gone, likely due to a mixture of factors, including cyclone activity, fishing gear impacts, urbanization, and river discharges,[10,13,25] although evidence suggests coral recovered recently.[35] Boat-based fisheries operating in backreef and forereef zones, which are dominated by fish and octopus catches (Figure 6), are unlikely to experience acute thermal mortality of the kind documented for intertidal invertebrates, since these subtidal habitats do not reach the tide-driven extremes recorded on the reef flat (Table S1). Instead, these fisheries are more likely to be affected indirectly and over longer timescales through the erosion of structural coral habitat that fish and octopus rely on for shelter and recruitment. This asymmetry is consistent with our fishery data showing that the most thermally extreme zones (reef flat

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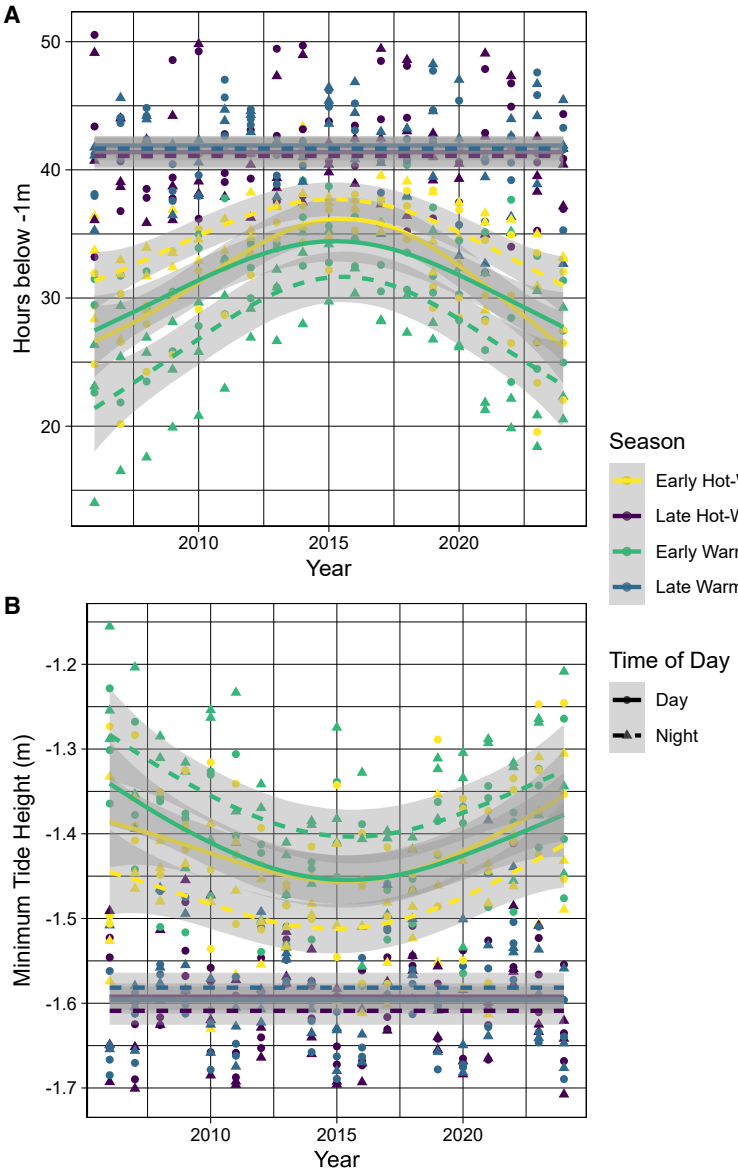


**Figure 5. Decadal trends of low-tide exposure duration and minimum depth**

(A and B) Hours spent below −1 m (relative to mean tide, TPXO9 tide model) and (B) minimum tide height (TPXO9 tide model) for each month at Salary Reef between 2006 and 2024 (18 years) across austral seasons (hot-wet, November-April; warm-dry, May–October) and daily sun cycles ($n$ = 456). Lines of fit are loess lines. Each point represents the monthly maximum hours below −1 m or minimum tide height (split by day and night), so that there are 24 data points each year (12 monthly calculations across day and night cycles).

See also Figures S7 and S8.

and shallow lagoon) are also where invertebrate harvest, particularly sea cucumbers, is concentrated. The hypothetical collapse of shallow-water reef environments would therefore directly threaten vulnerable gleaning fisheries, while climatic risk would be delayed and indirect for boat-based fisheries dependent on reef-associated fish and octopus.

Gleaning supports a diverse array of species critical to local food security and livelihoods, including both benthic macroinvertebrates and fish.[83,84] Among these, sea cucumbers represent a particularly important resource. The majority of sea cucumber biomass in our dataset was harvested from lagoon and nearshore reef flat habitats, the same zones where temperatures are elevated relative to deeper reef sites and where sub-daily thermal variability is greatest. Beyond our study area in Salary, there are major sea cucumber aquaculture pens in the lagoon and nearshore reef flats of the GRT.[39,85,86] A majority of sea cucumbers fished and collected are destined for the export market, providing an important source of income for fishers and gleaners.[53,85–87] Data on the thermal sensitivity of sea cucumbers are limited, but planktonic larval holothurian densities in southwestern Madagascar were the highest over the period between February and April, which corresponds with the hottest observed flat reef temperature.[85,88] This suggests early life stages may experience heat stress, although evidence from the region remains limited.

## Managing the coastal zone and promoting livelihoods in a warming world

Coupled with rapidly warming air and water temperatures in the WIO region,[1,16,18,89] hotter low tides may be in store for southwestern Madagascar. Our data were collected during a relatively low phase of the 18.6-year lunar tidal cycle, meaning logger observations underrepresent the thermal extremes that will characterize the next tidal maximum around 2033. Over a longer decadal horizon, sea level rise may alleviate heat exposure of tidal flats by increasing inundation hours, at the expense of lost gleaning opportunities during weak low-tide periods.[90] Because gleaning activity in southwestern Madagascar is most intensive during the hot intertidal shoulder seasons, the populations of gleaned species may face compounding pressures from harvest and heat stress simultaneously and during the same narrow windows. Gleaners themselves are already reporting declining yields attributable to warming, suggesting these dynamics may be already underway.[91,92] Finally, while beyond the scope of this paper, we raise the possibility of human physiological heat stress in gleaners fishing in the reef flat.

Previous work assessing the climate sensitivity and resiliency of reef fisheries in Madagascar identified the northwest as the

**Table 2. Distribution of fishing effort and catch biomass among geomorphic zones on Salary Reef**

| Geomorphic zone | Number of fishing trips | Total catch biomass (kg) | Mean catch biomass per trip (kg) | Mean CPUE (kg fisher$^{-1}$ h$^{-1}$) |
|---|---|---|---|---|
| Nearshore (includes Reef Flat) | 45 | 314.2 | 7.0 | 1.36 |
| Lagoon | 370 | 2,203.6 | 6.0 | 0.94 |
| Backreef | 20 | 81.5 | 4.1 | 0.80 |
| Reef crest | 714 | 3,379.2 | 4.7 | 0.90 |
| Forereef | 293 | 1,760.5 | 6.0 | 1.03 |

Values represent the number of recorded fishing trips, total catch biomass (kg), mean catch biomass per trip (kg), and mean CPUE for each geomorphic zone. See also Table S5.

most sensitive region to climate impacts due to elevated SST and solar irradiance but did not consider the importance of tidal regimes or reef microclimates on gleaning fisheries.[6,93] Active management and adaptation to climate change in the region will need to confront these realities of asymmetric thermal risk. MPAs in Madagascar, including the Soariake MPA within which our study site is located, currently do not account for different spatial use of different fishery types. Effective spatial management in coastal reef ecosystems will need to confront different use cases of reef zones that experience different magnitudes and timing of heat stress and fishing pressures. Shallow reef areas and the fisheries they support will experience heat stress sooner than deep reef habitats. Therefore, gleaning fisheries will require access to shallow reef zones within MPAs to be managed for their social resiliency. In addition, the promotion of alternative livelihoods to reduce fishing pressure will also be necessary, along with providing a livelihood portfolio in the case of heatwave-induced fishery collapse.

As the climate warms, the reef system of southwestern Madagascar will continue to experience more frequent, longer, and more intense heatwave events amplified by the semidiurnal, macrotidal system. On this reef system, where gender roles, socioeconomic security, and fishery styles are spatially separated, we also uncovered spatial separation in climate exposure. Climate adaptation and fisheries management that assume stationary extreme heat timing across spatially segregated fisheries therefore risk misidentifying risk windows for the most vulnerable human populations. Given that seagrass fish assemblages, which overlap with the reef flat and lagoon zones, provide more micronutrients than assemblages found on reefs,[54] hotter shallow and intertidal reefs may cause disproportionately severe impacts on the availability of nutrients to vulnerable human communities. Future work could also assess the extent to which socio-ecological systems will be impacted, especially when considering extremes and spatial structure.[94,95] By taking a fine-scale lens to reef thermal landscapes, we advance our spatiotemporal understanding of where extreme heat may be experienced most by reef organisms and, by extension, by the fishers that depend on these reef ecosystems.

## METHODS

### Study site

The study was conducted on Salary Reef (22.53°S, 43.25°E; Figures 1, S1, and S2), a fringing reef system located in southwestern Madagascar, approximately 100 km north of the region's major city, Toliara. This fringing reef system is part of the Mikea Coast and is distinct from the major, better-studied barrier reef off the coast of Toliara, GRT, because Salary receives little riverine input. The GRT has long been known to be influenced by the hydrology of the Onilahy and Fiherenana rivers, and excess sedimentation from upstream terrestrial activities such as mining and agriculture has partially contributed to the decline of the GRT.[13,68] However, Salary Reef is relatively uncoupled from terrestrial activity and is in better ecological condition than the GRT. This fringing reef system is composed of intertidal flats sloping to a sandy-bottomed lagoon varying 2–5 km in width and ~5–15 m in depth. The reef crest is periodically emersed during low-tide events, and complex reefs dominate the far-reef slope.[19,96] Southwestern Madagascar can be considered a meso- to macrotidal system—tidal ranges can extend up to 5.5 m (near Besalampy), exposing extensive reef flats and parts of the barrier/fringing reef crest. The Soariake MPA, managed by the Soariake Association with technical assistance from the Wildlife Conservation Society (WCS), was formally protected in 2015 to balance conservation and fishing and encompasses all of Salary Reef and the northern portion of the fringing reef system, but adherence by small-scale artisanal fishers is variable.[97] Most boat-based fishing activity occurs on the forereef and in the lagoon, while gleaning can occur both in the shore-adjacent reef flat and on the reef crest itself.

### Logger deployment and recovery

We deployed ten temperature loggers (ElectricBlue T7.3, Porto, Portugal—all IDs SALEB# "Salary ElectricBlue") between July 28 and August 10, 2023, distributed between four reef geomorphic zones (reef flat, lagoon, backreef, and forereef) between 2 and 4 m depth (Figures 1 and S1; Table 1). Geomorphic zones of each logger location were determined through field observation and further supported by the geomorphic zone layer in the Allen Coral Atlas.[98] Prior to deployment, we confirmed that temperature loggers were calibrated within 0.25°C of each other. We classified reef flat locations as representative of inshore intertidal gleaning sites, as we could not deploy loggers directly on the reef crest. Lagoon, backreef, and forereef sites represented boat-fishing locations. Additionally, we selected a site at the Salary Bay dive center to measure the air temperature at 2 m above ground. For all but the air temperature logger, we did not attempt to shade loggers from solar radiative warming,[99–101] so as to

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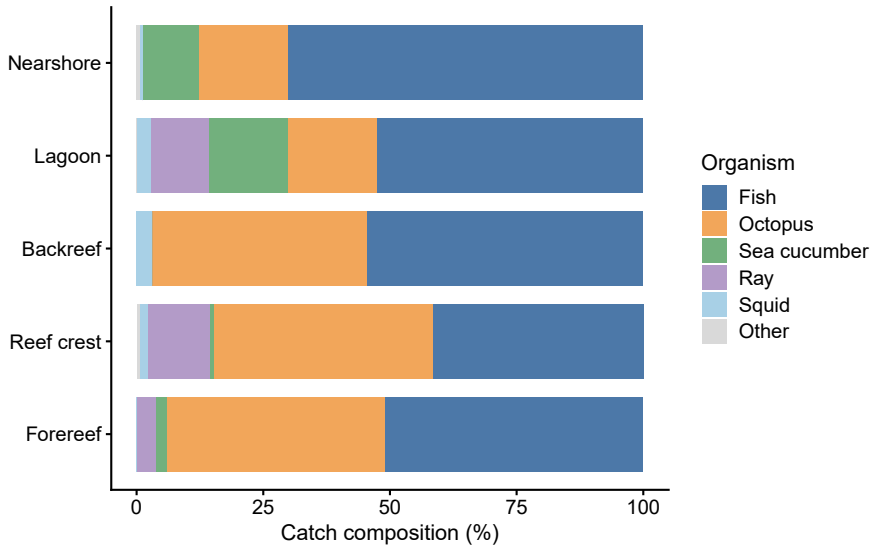


**Figure 6. Organism catch composition (%) across geomorphic zones on Salary Reef**

Bars show the proportional contribution of major harvested groups to total catch biomass within each geomorphic zone ($n$ = 1,442 trips total; see Table 2 for trip counts by zone). Less common taxa, including crabs, eels, and lobsters, were grouped into the "other" category.

replicate the microclimate or body temperature that may actually be experienced by exposed sessile marine organisms in each geomorphic reef zone.[102–104] Temperature data should therefore not be interpreted as seawater temperature, but as a record of potential benthic ectotherm body temperature. The simple use of seawater (or air) temperature to understand potentially stressful periods fails to account for the complexities of an organism's heat budget, even in submerged environments.

We affixed loggers to the reef using zip ties and Splash-Zone two-part marine epoxy (Modern Recreational Technologies, Hickory, NC, USA). We selected crevices for logger deployment to reduce breakage from wave action and to record temperatures of these reef refugia for many targeted fishery species. We recorded GPS coordinates with up to 5 m accuracy (Garmin eTrex 10) and recorded videos of logger placement (GoPro Hero8 Black) to facilitate recovery. To avoid accidental removal of loggers in this actively fished reef, we did not visually mark the locations of sensors. We relied on GPS coordinates, video footage, and local knowledge to recover loggers. Temperature logger accuracy was set to 0.1°C, recording every 15 min. We recovered five loggers after at least 1 year (Figure S1; Tables 1 and S2). Logger deployment and recovery were accomplished by freediving.

## Fishery data

To provide fisheries context for the study area, we analyzed fisheries-dependent catch data collected in the village of Salary, between July 29, 2023 and July 20, 2024. Catch monitoring was conducted by two trained local fish collectors using standardized KoboToolbox surveys that recorded fishing location, catch composition, catch weight, fishing effort, and crew size. Of 1,561 unique Salary fishing trips recorded across 182 sampling days during this period, 1,442 trips across 104 sampling days (92.4%) with identified reef-zone classifications were retained for analysis. Completed fishing trips with identified fishing locations were matched to reef geomorphic zones (nearshore, lagoon, reef crest, backreef, and forereef) based on local ecological knowledge. Many of these fishing locations are indicated with colored polygons in Figure 1, although not all fishing locations were geo-referenced on the map (Figure S1).

CPUE was calculated for each fishing trip as total catch biomass (kg) divided by trip duration (h) and the number of fishers participating in the trip and is expressed as kg fisher$^{-1}$ h$^{-1}$. Additional details regarding sampling protocols, data validation, and CPUE calculations are provided in Fortunato-Jackson et al.,[38] who used the same fishery dataset analyzed here. The studies involving humans were approved by Middlebury College Institutional Review Board. The studies were conducted in accordance with the local legislation and institutional requirements. The participants provided their written informed consent to participate in this study.

## Data analysis

### *Temperature data*

Of the ten temperature loggers deployed, we recovered five (four reef loggers and one air temperature logger) after at least 357 days (SALEB8, reef flat) and at most after 453 days (SALEB1). Although some loggers collected data for over a year, we focused our comparative site analysis only on dates where all four recovered water temperature loggers actively collected data (357 days).

To compare our logger-recorded reef temperatures against commonly used remote-sensed products, we further downloaded and extracted seawater temperature data from NOAA OISST [105] and Copernicus Global Physics Analysis[106] at −22.6°S, 43.25°E. OISST records sea surface temperatures were available at 1/4° resolution, while we selected Copernicus temperature records from a depth of 0.5 m at a 1/12° resolution. We calibrated our air temperature data against downscaled ERA5 models of air temperature using the *mcera5* R package.[107]

### *Tidal regime*

As no tide stations are available in southwestern Madagascar, we used the package *pyTMD*[108] in Python (v.3.10.15) to calculate tide heights at the coordinates −22.6°S, 43.25°E between the years 2006 and 2024. This timescale was chosen to encapsulate the 18.6-year lunar cycle to which short-term tidal cycles respond.[58] This decadal analysis further served to describe whether the tidal regime recorded in our 2023–2024 intertidal temperature data represents the long-term trend for this location. We used the TPXO9 (v.5, 1/30$^0$ resolution) atlas model of global tide constituents[109] and downloaded data at 1-min

resolution for a total of $n$ = 9,993,600 predicted data points. For some of our analysis, we grouped tide data by four seasons—early hot-wet (November–January), late hot-wet (February–April), early warm-dry (May–July), and late warm-dry (August–October). Initial exploration of the intertidal logger data indicated that distinct temperature regimes occurred along the four seasonal divisions listed above, and so, we processed some of our tidal data using this seasonality.

We used a custom script (see Note S1) to determine the relative tide height and tidal exposure regime of the intertidal temperature logger (SALEB8 Flat), based on significant drops in temperature correlated with rapid cooling or warming of temperature loggers when exposed to air or water.[110,111] We determined the intertidal temperature logger to have a height of −0.956 m (relative to average height) and +22 min behind the modeled tide series obtained via the *pyTMD* package. From this tide height, we reconstructed the immersion status of each time point from the intertidal temperature logger time series. When determining the decadal patterns of low-tide exposure, we used the rounded height of this logger (−1 m, relative average modeled height) as a threshold beyond which we calculated hours of exposure.

### *Statistical analysis*

All statistical analysis was completed in R (v.4.2.1). For cross-site comparisons, we filtered available water temperature datasets to only the dates that data had for all sites (from July 29, 2023 to July 20, 2024). We used a Kruskal-Wallis non-parametric test to determine if median site temperatures were different and then post hoc Bonferroni-adjusted Dunn's test package to determine pairwise site significance. When calculating post hoc pairwise comparisons between sites, we used a common window dataset of all site temperatures, rather than all temperature time points per site.

We used wavelet analysis to determine the temporal patterns in power spectra during the deployment period of our temperature data time series. By decomposing temperature periodicity on a time basis, this method allows for the detection of non-stationary periodicity in environmental time series and provides an advantage over traditional power spectra analysis.[112,113] We used the *WaveletComp* package to decompose and visualize the wavelet spectra using default Morlet wavelets.[114] Further details on wavelet analysis and interpretation are found in Note S2.

## RESOURCE AVAILABILITY

### Lead contact

Requests for further information and resources should be directed to and will be fulfilled by the lead contact, Andrew Villeneuve (drew.villeneuve@unh.edu).

### Materials availability

This study did not generate new unique reagents.

### Data and code availability

Data and code used to generate the analysis presented in this manuscript are freely available at Zenodo: https://doi.org/10.5281/zenodo.21709893.[115]

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## AUTHOR CONTRIBUTIONS

Conceptualization, A.R.V. and E.R.W.; methodology, A.R.V., M.B.-M., B.R., O.F.-J., and E.R.W.; formal analysis, A.R.V. and O.F.-J.; writing – first draft, A.R.V. and O.F.-J.; writing – review and editing, A.R.V., M.B.-M., B.R., O.F.-J., and E.R.W.; funding acquisition, M.B.-M. and E.R.W.; and project administration, M.B.-M., B.R., and E.R.W.

## DECLARATION OF INTERESTS

The authors declare no competing interests.

## DECLARATION OF GENERATIVE AI AND AI-ASSISTED TECHNOLOGIES IN THE WRITING PROCESS

During the preparation of this work, the authors used ChatGPT (GPT-4) to copyedit text and troubleshoot R and Python code originally written by the authors. After using this tool/service, the authors reviewed and edited the content as needed and take full responsibility for the content of the published article.

## SUPPLEMENTAL INFORMATION

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