LIMNOLOGY and OCEANOGRAPHY

ASLO

Limnol. Oceanogr. 70, 2025, 3127–3142

doi: 10.1002/lno.70172

RESEARCH ARTICLE

Climate change impacts to upwelling and shallow reef nutrient sources across an oceanic archipelago

Danielle L. Spring [1,2*] **Michael D. Fox,** [2] **J. A. Mattias Green,** [1] **Robin Guillaume-Castel,** [3] **Zoe Jacobs,** [4] **Ronan C. Roche,** [1] **John R. Turner,** [1] **Gareth J. Williams** [1*]

[1]Bangor University School of Ocean Sciences, Menai Bridge, Anglesey, UK; [2]Marine Science Program, Biological and Environmental Science and Engineering Division, King Abdullah University of Science and Technology, Thuwal, Kingdom of Saudi Arabia; [3]Université de Toulouse, LEGOS (CNES/CNRS/IRD/UPS), Toulouse, France; [4]National Oceanography Centre, Southampton, UK

Abstract

Upwelling delivers key nutritional and energetic subsidies to coral reef communities that affect the growth, abundance, and ecology of organisms across trophic levels. However, the cross-scale oceanographic and atmospheric drivers of localized upwelling on many reefs remain unresolved, limiting our ability to predict how climate change might disrupt upwelling patterns and impact reef communities across geographies. Using high temporal resolution (10 second) in situ temperature measurements collected over 18 months that encompassed the strongest positive Indian Ocean Dipole phase of this century, we demonstrate a highly nonlinear effect of climate-driven mixed layer depth on upwelling intensity across the latitudinal range of the Chagos Archipelago ($\sim$ 200 km). The exposure of shallow (10–25 m depth) reef communities to deeper upwelled waters was maximized when the mixed layer depth was shallower than $\sim$ 40 m, but virtually absent when the mixed layer depth was deeper than $\sim$ 60 m. By combining these temperature data with nitrogen stable isotopes ($\delta^{15}N$) from a common macroalga, we show these variations in upwelling correlate with altered nutrient sources that have direct measurable impacts on reef organisms across the Archipelago. We further show that over the past 40 years, positive phases of the Indian Ocean Dipole correlate with an anomalously deep surface mixed layer on these reefs, each time likely restricting upwelling. Given these extreme events are increasing in frequency under climate change, this poses the possibility of a markedly different upwelling regime across the Archipelago over the coming century, with currently unknown ecological consequences.

Across the global ocean, upwelling transports deep, cool, and nutrient-rich water to the shallows (Cushing 1989; Bakun 1990). This delivery of limiting nutrients to the well-lit upper water column facilitates primary production and underpins the success of higher trophic-level organisms (Pauly and Christensen 1995; Carr 2001). Crucially, climate change is disrupting patterns of upwelling by increasing ocean stratification (Li et al. 2020), driving spatial changes in upwelling-favorable winds (Bakun et al. 2010) and altering the seasonality of upwelling (Wang et al. 2015). Modeling studies suggest that disruptions to upwelling regimes will continue into the future (Wang et al. 2022; Xiu et al. 2018), with unknown consequences for marine ecosystems and the human communities they support.

Highly biodiverse tropical coral reefs are particularly vulnerable to climate change impacts (Hughes et al. 2017; Williams and Graham 2019). Reefs globally are suffering the damaging effects of marine heatwaves, deoxygenation, and changes to water column stratification (Johnson et al. 2021; Diaz et al. 2023; Wyatt et al. 2023). Against this backdrop of global change, upwelling acts as a key structuring force of reef communities, delivering limiting nutrients (Wolanski et al. 1988; Gove et al. 2006; Aston et al. 2019) and supporting primary production by autotrophic organisms, including phytoplankton and macroalgae (Radice et al. 2019; Johnson et al., 2020).

*Correspondence: d.spring@bangor.ac.uk, g.j.williams@bangor.ac.uk

Associate editor: David Baker

Upwelling also directly supports primary consumers, such as mixotrophic corals and planktivorous fish, fueling their production through the transfer of plankton and particulate organic matter to the shallows (Leichter and Genovese 2006; Fox et al. 2018; Williams et al. 2018; Miller et al. 2019). These direct effects, in turn, support higher trophic-level consumers by boosting their prey base (Morais and Bellwood 2019). As such, changes in upwelling regimes have the potential to impact reef communities across trophic levels.

Mixotrophic reef-building corals benefit from upwelling in several ways. Upwelling bolsters autotrophic nutrition through the delivery of inorganic nutrients, which can be assimilated by endosymbiotic algae within coral tissues (Becker et al. 2021). The transport of particulate and planktonic food subsidies associated with upwelling—hereafter referred to as "pelagic subsidies"—enhances heterotrophic resource availability and therefore feeding capacity (Radice et al. 2019). Mixotrophic corals can adapt their trophic strategies in response to changes in energetic resources (Fox et al. 2018; Williams et al. 2018; Sturaro et al. 2021). Further, temporary cooling driven by upwelling can provide thermal relief to corals during marine heatwaves and in a warming ocean (Wall et al. 2015; Schmidt et al. 2016; Tkachenko and Soong 2017; Randall et al. 2019; Wyatt et al. 2020). Yet, our understanding of how the different aspects of upwelling—food, nutrients, and cooling—interact to structure reef systems is limited. Upwelling can benefit coral growth and survivorship (Stuhldreier et al. 2015; Fox et al. 2023) or exacerbate bleaching through increased symbiont demands on coral hosts in response to nutrient enrichment (Jantzen et al. 2013; Eidens et al. 2014; DeCarlo et al. 2020). Cold water intrusions can even trigger cold-water bleaching due to reduced coral metabolic function (Marangoni et al. 2021; Foreman et al. 2024). The effects of upwelling on coral reef communities appear highly context dependent (Spring and Williams 2023), and the biophysical interactions on reefs across different geographies and upwelling regimes remain uncertain.

The drivers of upwelling regimes around coral reefs are complex, consisting of cross-scale and interacting physical processes. Upwelling can occur through wind-driven Ekman transport, by internal waves propagating along a density boundary, and in the wake of current flows (Leichter et al. 1996; Lowe and Falter 2015; Gove et al. 2016; Reid et al. 2019). Tidally driven internal bores (Leichter et al. 1996), mesoscale eddies (Wyatt et al. 2023), regional winds (DeCarlo et al. 2021) and surface currents interacting with island topography (Gove et al. 2006) can interact with one another to structure upwelling regimes across geographies. Oscillations in regional climate modes, including the El Niño Southern Oscillation and large-scale processes linked to the monsoon and Indian Ocean Dipole, drive changes in upwelling regimes across ocean basins (Schott and McCreary 2001; Fox et al. 2023). Local-scale forces and physical attributes of individual reefs can also interact with broad-scale oceanographic drivers to create intra- and inter-island gradients in upwelling at relatively small spatial scales (Williams et al. 2018; Aston et al. 2019; Fox et al. 2023). To improve our ability to accurately predict and model upwelling impacts on coral reefs, a targeted, mechanistic assessment of the physical drivers that regulate upwelling is required, spanning regional, archipelago, and island scales.

Here, we quantify the upwelling regime across the Chagos Archipelago, a remote atoll chain in the central Indian Ocean. The Archipelago, which has been subject to ongoing political and legal discussions regarding sovereignty and resettlement, currently lacks a resident local human population and comprises one of the world's largest marine protected areas (Hays et al. 2020). The Chagos Archipelago therefore serves as a natural laboratory for studying the biophysical drivers of coral reef state in the absence of confounding direct local human impacts. We use in situ temperature data collected across ~ 200 km to quantify spatial and temporal patterns in localized upwelling, and statistical models to identify the principal atmospheric and oceanographic drivers of these patterns. Combining this with stable isotope analysis of a common macroalga, we demonstrate that large-scale climatic processes directly influence reef communities. Using ocean and climate reanalysis models, we extend our analysis to explore trends in the principal correlates of upwelling over the past 40 years, showing that extreme positive Indian Ocean Dipole events trigger conditions which restrict upwelling on shallow reefs across the Chagos Archipelago. With these extreme events becoming more frequent and expected to increase under global warming (Cai et al. 2009, 2013), associated disruptions to existing upwelling regimes could have a dramatic impact on the structure and function of reef communities across the global ocean.

Methods

Quantifying upwelling and reef slope profiles

To quantify the upwelling regime across the Chagos Archipelago (Fig. 1), we deployed temperature loggers at 15 sites on the fore reef habitat (the reef slope facing the open ocean) of three atolls (Peros Banhos; $n = 6$, Salomon; $n = 4$ and Egmont; $n = 5$) spanning the latitudinal gradient of the Archipelago in the central Indian Ocean ($n = 14$ sites where temperature data were retrieved; *see* Supporting Information Table S1 for detailed site information). Sites were haphazardly selected to capture all major cardinal directions around each atoll. Temperature measurements were recorded using Sea Bird Electronics© SBE-56 temperature loggers (0.002°C accuracy), with an individual logger attached to the reef substrate at each of three depths: 10 m (shallow), 17.5 m (mid) and 25 m (deep) at each site. At two sites, the full logger array was not retrieved, restricting upwelling assessment to only mid (SA2) and deep (EG1) depths (Fig. 1). The tidal range across the Chagos Archipelago is typically less than 1 m (Pugh and Rayner 1981), and

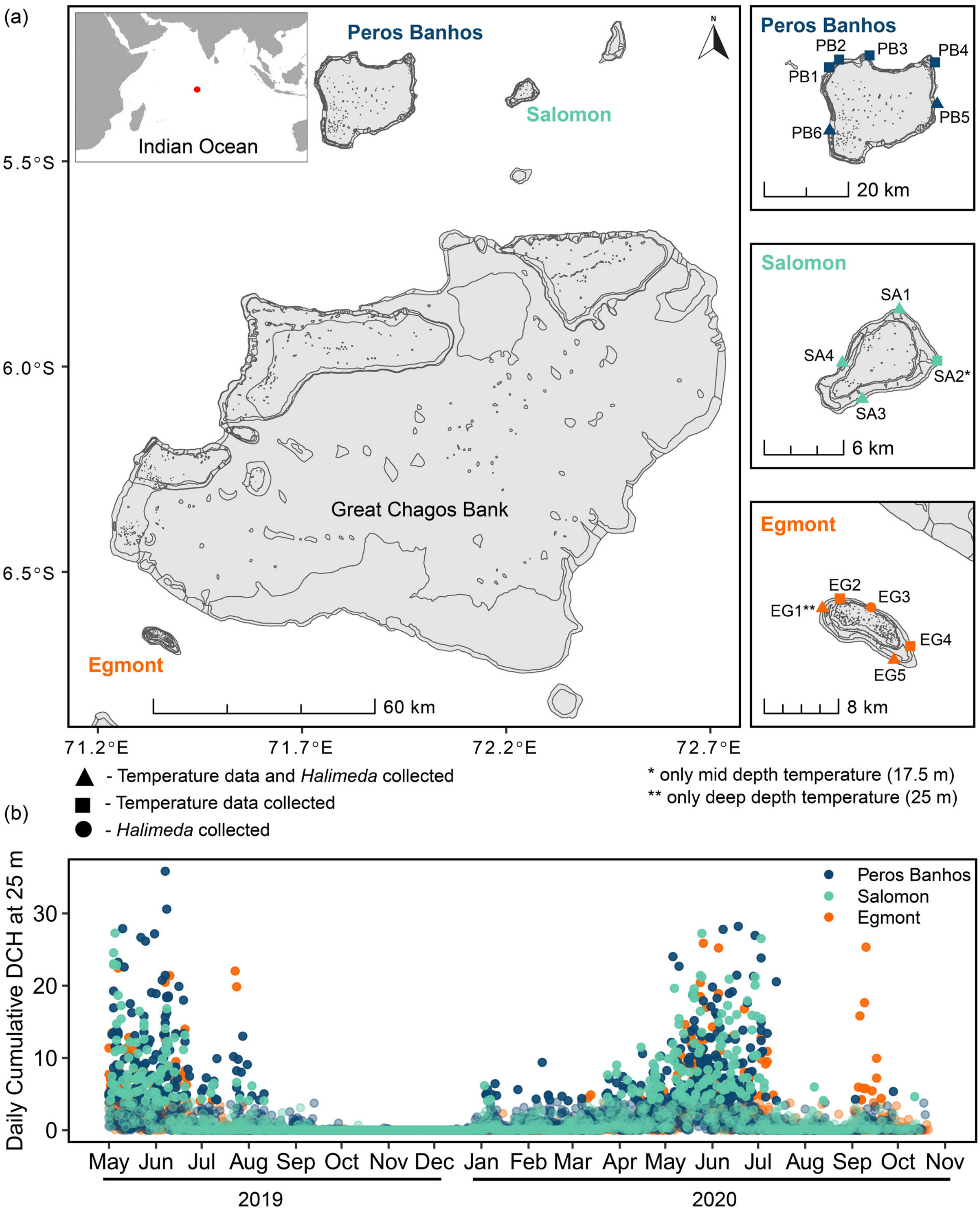

Fig 1. (**a**) Study sites around the Chagos Archipelago in the central Indian Ocean. Colored shapes on maps indicate data collection sites. A single temperature logger (10 second interval, 0.002°C accuracy) was attached to the reef substrate at each of three depths (10, 17.5, and 25 m) at each site to quantify upwelling on the fore reef over 539 days between May 1, 2019 and October 21, 2020. Samples of the common reef macroalga *Halimeda* were collected in 2019 and again in 2021 for stable isotope analysis of nitrogen ($\delta^{15}N$) to link upwelling with nutrient delivery across the Archipelago. (**b**) Daily cumulative Degree Cooling Hours (DCH) recorded by in situ temperature loggers at 10 second resolution (0.002°C accuracy) attached to the benthos at three atolls (4–6 sites per atoll).

depths were selected based on the restrictions of working on open-circuit SCUBA with standard air mix in a remote setting. All loggers recorded temperature every 10 seconds. Loggers were deployed between April 11, 2019 and April 26, 2019 and ran until batteries expired. Logger time series were truncated for comparability across all sites, running for 539 days between May 1, 2019 and October 21, 2020. An example of the full raw temperature time series and associated Degree Cooling Hours for Site SA1 can be viewed in Fig. 2, with additional representative sites PB4 and EG5 displayed in Supporting Information Fig. S1. Power spectral density analyses using Welch's method (Welch 1967) were conducted to identify the periodicity of major frequencies of oscillation within the temperature time series and their associated strengths. We used a window length of 7.59 days (i.e., 2^{16} of 10 second interval data) and applied a Hamming Window, with an overlap of 5.69 days.

We quantified upwelling from the in situ temperature data using the Temperature Stratification Index method (Guillaume-Castel et al. 2021). In summary, a location-specific threshold for what constitutes an upwelled cold pulse is determined, calculated from the National Center for Environmental Prediction Global Ocean Data Assimilation System reanalysis product (NCEP/GODAS; Behringer and Xue 2004) (*see* Supporting Information for further details). Upslope-only propagation (i.e., not downwelling) of deep colder water recorded by the loggers across depths at each site triggers anomalous Temperature Stratification Index values, and a cold pulse is identified. The magnitude and duration of cold pulses were used to calculate Degree Cooling Hours—the magnitude of a cold pulse multiplied by its duration—which are then summed over each 24 hour period to give daily cumulative Degree Cooling Hours for each site, in units of °C hours (Guillaume-Castel et al. 2021).

Reef slope steepness is known to affect the refraction and upward propagation of vertical movement of water masses (Gove et al. 2016; Davis et al. 2020). To our knowledge, high-resolution deep-water bathymetry is not publicly available for the Chagos Archipelago. We calculated shallow reef slope steepness at each site using a handheld depth transponder (Garmin Montana 650T, ± 3 m accuracy) running perpendicular to shore to ~ 70 m depth.

Measuring upwelling impacts on reef biological processes

Stable isotope analysis of nitrogen (δ^{15}N) within benthic macroalgal tissue is a reliable tool to assess primary nitrogen sources to coral reefs (Cohen and Fong 2005; Dailer et al. 2010; Miller et al. 2019; Fox et al. 2023). To determine whether variation in upwelling resulted in a measurable change in the dominant available nitrogen in the shallows, we collected *Halimeda* sp. (hereafter *Halimeda*) from the benthos at the same depth and within 30 m horizontally from each temperature logger. *Halimeda* samples were collected in April 2019 upon deployment of the loggers ($n = 10$ replicate samples at each of the three depth strata per site) and (following a delay due to the COVID-19 pandemic) in November 2021 upon logger retrieval. Due to restrictions caused by the pandemic, a full second suite of algal samples was not retrieved ($n = 8$ sites; Peros Banhos = 2 sites, Salomon = 3 sites, Egmont = 3 sites). Samples were transported on ice and frozen at −20°C before processing. In the laboratory, the upper 2–4 segments of branch tips from each sample were removed, cleared of epiphytes, and dried at 60°C for 48–72 h. *Halimeda* produces new segments in a vertical, "upward" fashion from the base of the thallus, and the upper segments therefore represent the most recent period of growth (Vroom et al. 2003). Samples were homogenized but not decalcified before being analyzed for δ^{15}N. Bulk tissue δ^{15}N values were measured via EA-IRMS using a Costech 4010 elemental analyzer coupled to a Thermo Scientific Delta V Plus isotope ratio mass spectrometer at the University of New Mexico Center for Stable Isotopes (UNM-CSI). Nitrogen isotope values are reported as delta (δ) values in parts per thousand, or per mil (‰). All samples were calibrated against the internationally accepted standard (atmospheric N_2) and standard deviations of in-house reference materials were < 0.2 ‰ for δ^{15}N values.

To test for spatial and temporal changes in *Halimeda* δ^{15}N values across years and contrasting seasonal phases of upwelling, we built a linear mixed-effects model using the *lme4* package in R (www.r-project.org). We included year (2019 vs. 2021), depth (10, 17.5, and 25 m) and atoll (Peros Banhos, Salomon, Egmont) as fixed effects, and an interaction term between year and depth. We incorporated site as a random effect to account for the fact that multiple replicate samples were taken from each site and to model the variability between sites as a random component in the model, while treating atoll as a fixed effect, thus accounting for the hierarchical structure in our data. Only sites where replicate *Halimeda* samples were collected in both years ($n = 8$ sites: Peros Banhos, $n = 2$; Salomon, $n = 3$; Egmont, $n = 3$) were selected for this analysis. The model was fit using restricted maximum likelihood estimation, and we assessed model fit and convergence by checking residual plots and variance components. The significance of fixed effects was evaluated by examining the estimated coefficients, standard errors, and 95% confidence intervals.

Quantifying the atmospheric and oceanographic drivers of upwelling

To explore the atmospheric and oceanographic drivers of upwelling across the Chagos Archipelago, we used boosted regression tree (BRT) modeling. BRT is an additive regression modeling approach which combines machine learning decision trees (Breiman 2011) with boosting to reduce predictive error (Elith et al. 2008). Rather than attempting to fit a single parsimonious model, BRT combines large numbers of regression trees by sequentially fitting a new tree to the residuals of the previous tree (Elith et al. 2008; Jouffray et al. 2019). This

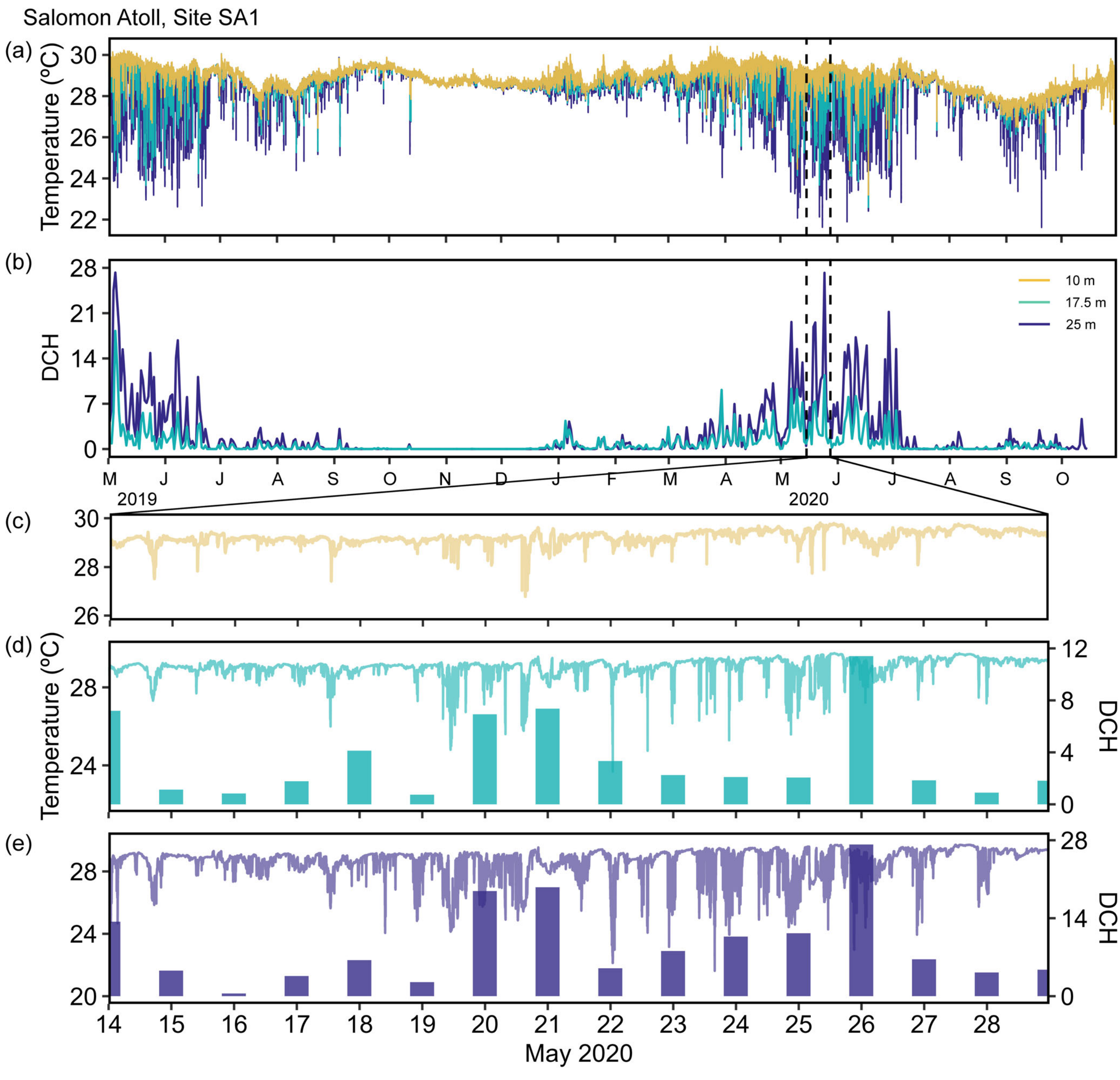

Fig. 2. Temperature time series for representative site SA1 on Salomon Atoll in the Chagos Archipelago from May 2019 to October 2020 (**a**), with associated calculated daily cumulative Degree Cooling Hour (DCH) metric over the same period (**b**). Full time series broken down by individual loggers in depth-stratified array (**c–e**), with associated DCH at 17.5 and 25 m depicted as vertical bars. Note difference in secondary y-axes scales in panels **d** and **e**. No DCH bars are shown for the 10 m plot (**c**) as this depth was used as the reference baseline for calculating DCH at 17.5 and 25 m depth (see "Methods" section).

ensemble method has superior predictive performance compared with traditional classification tree modeling methods, as it can fit complex nonlinear relationships, deal with missing predictor data, and handle mixed data types (Elith et al. 2008). We used BRT to examine the relative influence of each predictor on our observed spatial and temporal patterns in upwelling, using Degree Cooling Hours as the response variable.

Fourteen predictor variables were selected that represent known climatic drivers of upwelling variability and to account for our spatial dimensions of sampling within and between atolls and across depths (*see* Supporting Information Table S2 for details about each predictor variable, our justification for their inclusion in the model-fitting process and data sources). Prior to model-fitting, the continuous predictors were assessed for collinearity using pairwise Pearson's correlation coefficients ($r = < 0.8$ for all comparisons and therefore all were included in the model-fitting process). For predictor variables available at a monthly resolution, values were repeated for each day in each given month.

Degree Cooling Hours were converted to integers, and a Poisson distribution was used to model variation in upwelling across our study period. All statistical analyses were conducted using R v. 4.3.3 (R Core Team 2020). Statistical scripts and associated data are available on GitHub (https://github.com/daniellelucyspring/Upwelling-drivers). We built BRT models using the *gbm.step* routine in the *dismo* package v. 1.1-4 (Hijmans and Elith 2017) for R, with graphical outputs created using the *ggBRT* suite of functions (Jouffray et al. 2019). See Supporting Information for details on quantifying model performance, cross validation, and temporal autocorrelation.

Given the strong influence of mixed layer depth on upwelling (see Results), we reran our BRT modeling routine, replacing Degree Cooling Hours with mixed layer depth as the response variable to ask: if mixed layer depth is driving variability in upwelling, what is driving variability in mixed layer depth? We built this second BRT model using a gaussian distribution, with optimized model parameters (*see* Supporting Information). To strive for model parsimony, sea surface height was removed a priori from the model-fitting process. While sea surface height is a useful indicator of the depth of the surface mixed layer (Rebert et al. 1985), these variables vary synchronously with one another in a highly correlated manner in response to external atmospheric and oceanographic forcings. Sea surface height does not directly cause changes in mixed layer depth. Given the objective of this study was to identify causal drivers of mixed layer depth variability, sea surface height—as a correlated but not causal parameter—was removed from the modeling routine. As mixed layer depth estimates are available for the Chagos Archipelago since 1980, mean monthly values for all other predictors were obtained from January 1980 to December 2023, and the BRT model was constructed on data from across this temporal period to maximize replication.

For both BRT models, the relative influence of each predictor variable was determined by the number of times it was selected for splitting trees, weighted by the resulting squared improvement to the model averaged over all trees (Friedman and Meulman 2003). To visualize the most important conditional response–predictor relationships, partial dependency plots with fitted functions and 95% confidence intervals were built from 1000 bootstrap replicates (Jouffray et al. 2019). These partial dependency plots were created for the variables which had a relative influence greater than that expected by chance (100 divided by the number of variables, here 7.14%), with their influence then rescaled to 100% (Müller et al. 2013; Jouffray et al. 2019).

We plotted mixed layer depth climatology compared with our recording years (2019, 2020) to assess the broader representativeness of our time series. We also visualized water column temperature profiles from the GODAS reanalysis product for all years since 1980 and calculated mean mixed layer depth for each year, comparing this to our recording years (2019, 2020) (Supporting Information Fig. S4).

Results

Spatiotemporal patterns of upwelling across the Chagos Archipelago

We observed an overall seasonal pattern in Degree Cooling Hours across the three atolls, with upwelling peaking in May and June of boreal summer (Fig. 1b). Daily cumulative Degree Cooling Hours (hereafter Degree Cooling Hours) recorded at the deepest logger (25 m) peaked at 35.8 °C hours at Peros Banhos (June 2019), 27.3 °C hours at Salomon (May 2020), and 25.9 °C hours at Egmont atoll (May 2020). Daily cooling was highly variable; during peak upwelling months of May and June (pooled over both 2019 and 2020), Degree Cooling Hours across all atolls averaged ($\pm$ 1 SD) 4.38 $\pm$ 5.17. The maximum daily temperature range recorded was 7.66°C on the Northern side of Peros Banhos. During the peak upwelling months of May and June, mean site-level Degree Cooling Hours were similar at Salomon and Egmont (ranging from 4.5 to 6.7 and 3.2 to 4.6, respectively), but Peros Banhos experienced a greater inter-site range in cooling (3.1 to 7.6).

Power spectral density analysis revealed strong semi-diurnal tidal frequencies, suggestive of internal wave forcing across the Archipelago (Supporting Information Fig. S3). Across all sites and all atolls, the M2 tidal signal was the prominent periodicity across all loggers, with the principal lunar diurnal frequency (O1) also appearing at all sites.

Broad- and local-scale predictors of upwelling across the Chagos Archipelago

The atmospheric and oceanographic predictor variables included in our model (Supporting Information Table S2) explained 57.7% cross-validated predictive deviance in Degree Cooling Hours, with six of the variables accounting for 52.0% of this (Fig. 3). See Supporting Information Table S3 for model parameter settings and Supporting Information Table S4 for the relative contribution of all predictors to overall model performance. Mixed layer depth (calculated as a 0.8°C temperature deviation from the surface; Fiedler 2010; Fox et al. 2023) was the strongest predictor of Degree Cooling Hours, with a relative influence of 31.4%. We observed mixed layer depth to have a highly nonlinear effect, whereby the exposure of shallow (< 25 m) reef communities to deeper upwelled waters was maximized when the mixed layer depth was shallower than $\sim$ 40 m (Fig. 3a). When the mixed layer depth was deeper than $\sim$ 60 m, Degree Cooling Hours were virtually absent, indicating a lack of exposure of shallow reef communities to deeper upwelled waters. Site was the second most influential predictor, with a relative influence of 20.8% (Fig. 3b). This suggests that site-level processes are influencing upwelling through drivers not captured by the remaining predictors included in our model. The model suggests that greater upwelling can be expected with greater sea-level pressure (14.7% relative influence), where an inverse barometric effect leads to a lower sea level. However, low replication of data points at low sea-level pressure resulted in large error for this predictor (Fig. 3c). The effect of depth (12.1% relative influence) met our expectations (*see* Supporting Information Table S2), demonstrating that deeper depths are more exposed to upwelled waters than shallower depths (Fig. 3d). Across all atolls, deep loggers (25 m) received 107% greater total Degree Cooling Hours over the entire time series than mid loggers (17.5 m). Variation in Degree Cooling Hours explained by zonal current velocity (11.6% relative influence) suggests that eastward flowing currents result in greater upwelling (Fig. 3e). Zonal winds (9.4% relative influence) indicate a slight increase in upwelling with decreased wind velocities, and with westerly winds (Fig. 3f). Contrary to our expectations, the remaining local-scale variables of cardinal direction and our estimates of reef slope

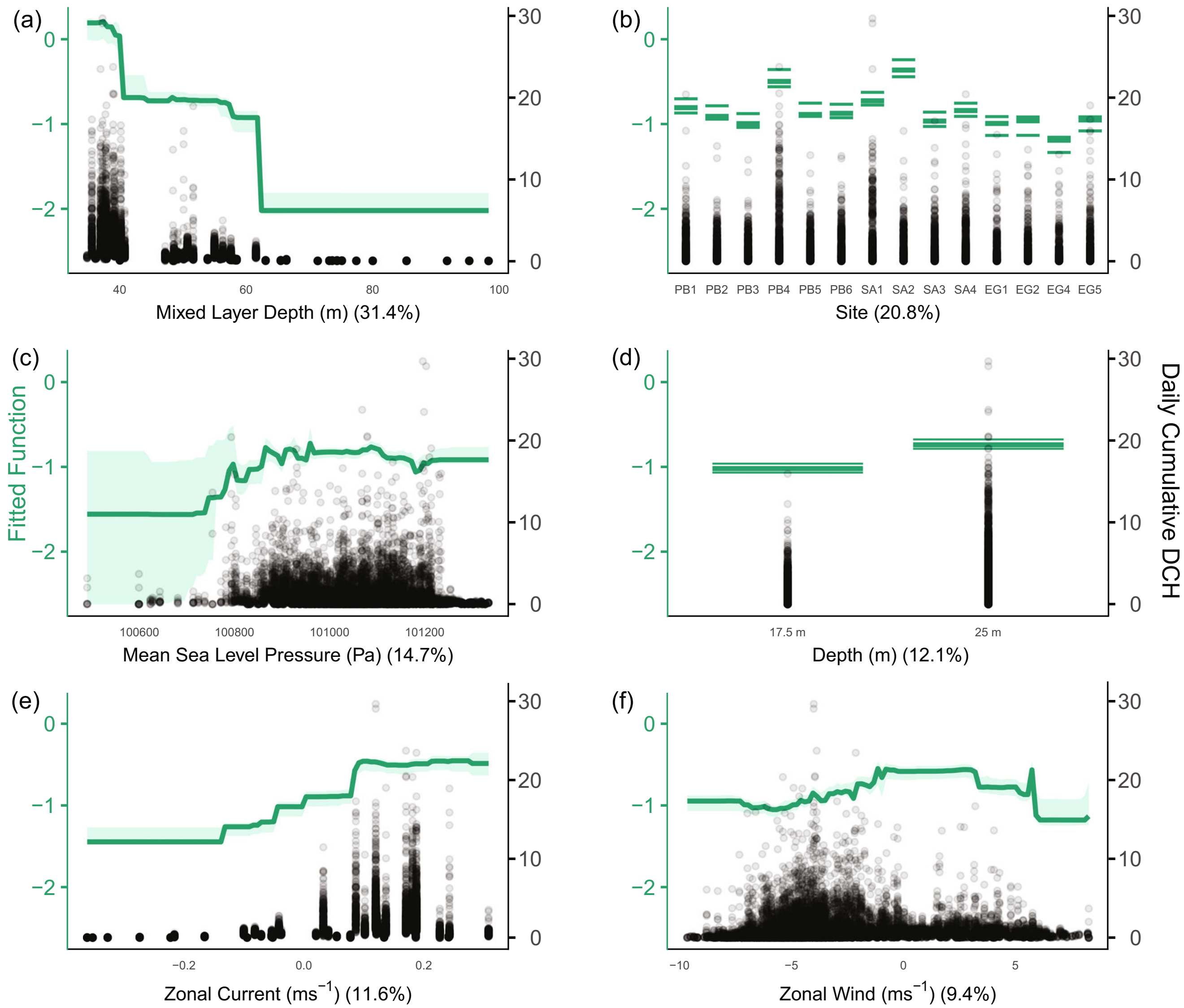

Fig. 3. Partial dependency plots showing the predicted relationships between Degree Cooling Hours and significant predictors (**a–f**) included in the model-fitting process (green lines); 95% confidence intervals are shown with a green ribbon for continuous predictors (**a**, **c**, **e**, **f**) and the interquartile range is shown with finer green lines around the thicker median line for categorical predictors (**b**, **d**) (obtained from 1000 bootstrap iterations). Faded black points show the fitted values for each predictor. In each case, the response–predictor relationship is shown while holding all other predictors in the model at their mean. The relative contribution of each predictor to overall cross-validated predictive deviance is reported in parentheses.

steepness (although coarse) were poor predictors of Degree Cooling Hour variability.

Predictors of mixed layer depth variability

Our second BRT model explained 70.5% of the cross-validated predictive deviance in reanalysis estimates of mixed layer depth (Fig. 4). Three variables significantly predicted variation in mixed layer depth: East–West Zonal Wind (60.3% relative influence), Indian Ocean Dipole mode (20.9% relative influence) and North–South Meridional Wind (18.8% relative influence). All three variables are strongly linked with the monsoon cycle and Indian Ocean Dipole; when strong easterlies blow, mixed layer depth has a greater probability of being deeper (Fig. 4a). Conversely, when zonal winds are weak, our models show the surface mixed layer to be shallow (~ 20 m) (Fig. 4a). Northerly winds and positive phases of the Indian Ocean Dipole also induce a deeper mixed layer (Fig. 4b,c). Notably, the strongest positive Indian Ocean Dipole phase of this century occurred in 2019 while we were recording in situ temperatures. Given that a deep (~ 60 m) mixed layer acts to restrict the exposure of deeper upwelled waters to shallow (< 25 m) reefs across the Chagos Archipelago (Fig. 3a), and strong positive dipole phases act to deepen the mixed layer (Fig. 4b), we next explored the link between positive dipole phases and anomalously deep mixed layers over the past half century.

We plotted phases of the Indian Ocean Dipole over the past 40 years, and overlayed anomalously deep (≥ 60 m) surface mixed layers during the months of October and November, when the surface mixed layer is usually shallow in the Chagos Archipelago, and when positive dipole events ordinarily occur (Xu et al. 2021). This revealed that during all extreme positive Indian Ocean Dipole events over the last half century, the surface mixed layer in the Chagos Archipelago was depressed to > 60 m depth (Supporting Information Fig. S5). Given our model results (Fig. 3a), this suggests that the shallow reef communities across the Archipelago were not exposed to deeper upwelled waters during all strong positive Indian Ocean Dipole phases since 1980.

To assess the representativeness of our survey years over broader timescales, we plotted monthly mixed layer depth climatology estimates since 1980 (Fig. 5) (*see* Supporting Information Fig. S4 for an example of the full water column temperature profiles for Peros Banhos). Our 2020 survey year was largely a representative year, with an annual mean (± 1SD) mixed layer depth of 46.4 ± 10.2 m, 25% deeper than the long-term mean of 37.2 ± 15.5 m. In 2019, which experienced the strongest positive Indian Ocean Dipole phase since the turn of the century, the annual mean mixed layer depth was 56.0 ± 18.7 m, 51% deeper than the long-term mean. This anomaly was particularly pronounced from September to December, where the mean mixed layer depth (79.9 ± 10.7 m) was 113% deeper than the long-term mean for this period (37.6 ± 17.6 m). The positive Indian Ocean Dipole event of 2019 peaked in October, and—presumably because of a lag effect—mixed layer depth in the following month of November was depressed to 91.8 m, a 206% increase on the 40-yr mean (30.0 ± 16.3 m) and the deepest it has been since records began in 1980. We found positive Indian Ocean Dipole events to coincide with anomalously deep mixed layers across the Chagos Archipelago throughout the past 40+ years of available mixed layer depth estimates (Supporting Information Fig. S5).

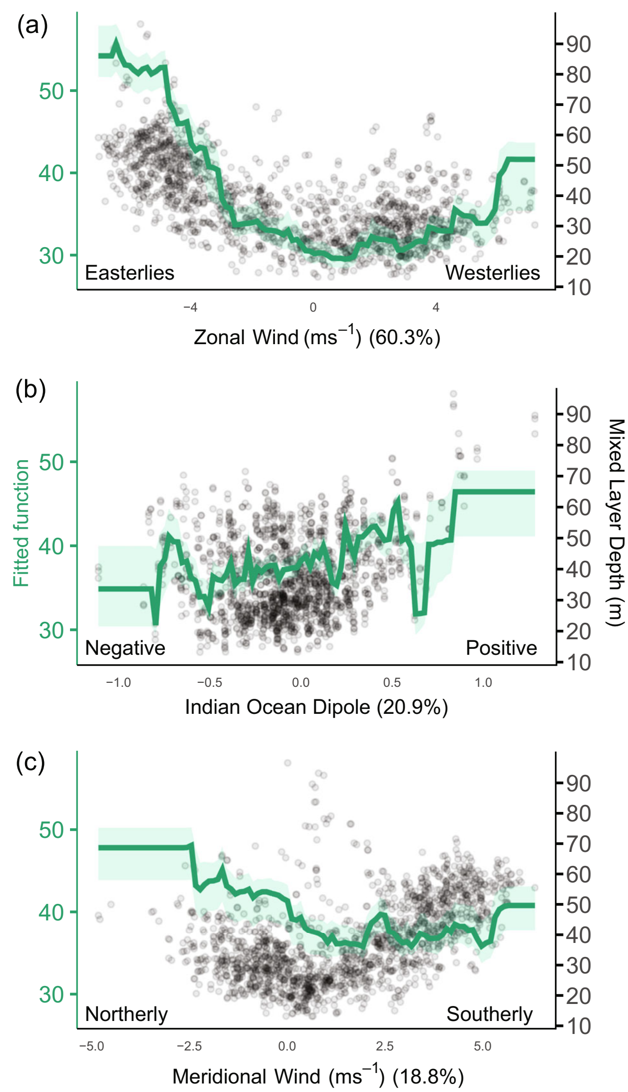

Fig. 4. Partial dependency plots showing the predicted relationships between mixed layer depth and significant predictors (**a–c**) included in the model-fitting process (green lines); 95% confidence intervals are shown with a green ribbon (obtained from 1000 bootstrap iterations). Faded black points show the fitted values for each predictor. In each case, the response–predictor relationship is shown while holding all other predictors in the model at their mean. The relative contribution of each predictor to overall cross-validated predictive deviance is reported in parentheses.

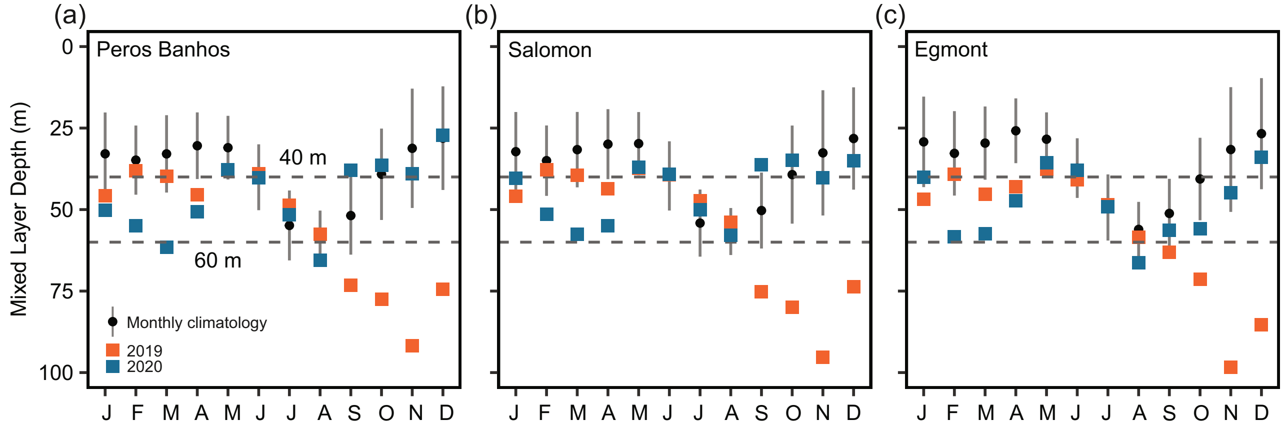

Fig. 5. Mean monthly climatological mixed layer depth estimates (± 1 SD) from the GODAS reanalysis product in black (psl.noaa.gov/data/gridded/data.godas.html), and monthly mixed layer depth values for 2019 and 2020 displayed in orange and blue, respectively, for (**a**) Peros Banhos, (**b**) Salomon, and (**c**) Egmont atolls in the Chagos Archipelago. Horizontal dashed lines denote 40 and 60 m, the depths identified through our boosted regression tree modeling as key thresholds for enhanced or reduced upwelling on shallow reefs (< 25 m), respectively.

Impacts on shallow reef biological processes

We used stable isotope analysis ($\delta^{15}N$) of a common benthic macroalga to quantify whether large-scale dynamics in upwelling impact benthic communities across atolls, sites, and depths in the Chagos Archipelago. *Halimeda* $\delta^{15}N$ values were on average 1.5‰ greater in November 2021 compared to April 2019 (mean $\delta^{15}N$ in 2019 4.3‰; mean $\delta^{15}N$ in 2021 5.8‰; Fig. 6c). There was a significant effect of "year" (estimate = 1.28, SE = 0.095, $t = 13.52$, $p < 0.0001$), with enriched $\delta^{15}N$ values in 2021 compared to 2019 (Fig. 6d). Depth had a significant effect only at the shallow depth (estimate = −0.19, SE = 0.091, $t = -2.07$, $p = 0.039$), indicating that shallow depths (10 m) had lower $\delta^{15}N$ than mid or deeper depths. There was a significant interaction between year and depth ($F_{[2,412]} = 5.82$, $p = 0.003$), with stronger increases in $\delta^{15}N$ values from 2019 to 2021 at shallow and mid-depths, compared to deeper depths. The effect of atoll was not significant. See Supporting Information Table S5 for full model summary output. In April 2019 (initial *Halimeda* collection), mean mixed layer depth across all atolls was 44.0 ± 1.3 m, 53% deeper than the average for this time of year, and deeper than the ~ 40 m threshold we identified that induces peak Degree Cooling Hours on shallow (< 25 m) reefs across the Archipelago (Fig. 3a). By contrast, November 2021 (second *Halimeda* collection and when *Halimeda* had enriched $\delta^{15}N$ values) had an anomalously shallow mixed layer depth across atolls (18.0 ± 2.6 m), 43% shallower than the monthly climatological mean and likely resulting in (based on our model results) enhanced localized upwelling across the Archipelago.

Discussion

Cross-scale oceanographic and atmospheric drivers of localized upwelling regimes remain unresolved on many reefs, leaving us unable to accurately predict how they may alter under climate change. Here, using high-resolution (10 second) in situ temperature measurements across ~ 200 km over 18 months in the central Indian Ocean, we reveal the strongest predictors of upwelling across an archipelago reef system. Critically, we demonstrate a highly nonlinear threshold effect of mixed layer depth on the exposure of shallow (< 25 m) reef communities to deeper upwelled waters. Exposure to upwelling was maximized when the mixed layer depth was shallower than ~ 40 m, but virtually absent across shallow reefs of the entire archipelago when the mixed layer depth was deeper than ~ 60 m. We further show that over 40 years of data, positive phases of the Indian Ocean Dipole drive an anomalously deep surface mixed layer, thereby linking broad, basin-scale climate variability with localized reef upwelling. By combining these temperature data with nitrogen stable isotopes from a common benthic macroalga, we show that regional variations in upwelling can have a direct, measurable impact on shallow reef organisms.

Cross-scale physical processes driving upwelling variability across the Chagos Archipelago

We found that the depth of the surface mixed layer was the most influential predictor of variations in the exposure of shallow reef communities to deeper upwelled waters across the Chagos Archipelago. Studies from other geographies show that a shallow surface mixed layer enhances upwelling on upper reef slopes. Leichter et al. (2012) observed internal wave-driven upwelling around Moorea during periods of strong stratification and a shallow mixed layer. Fox et al. (2023) found that mixed layer shoaling and sub-surface current acceleration increased upwelling at Palmyra Atoll during the 2015 El Niño. Wyatt et al. (2020) also linked shallow mixed layers to internal wave-driven upwelling that reduced heat stress during a pan-tropical marine heatwave in the

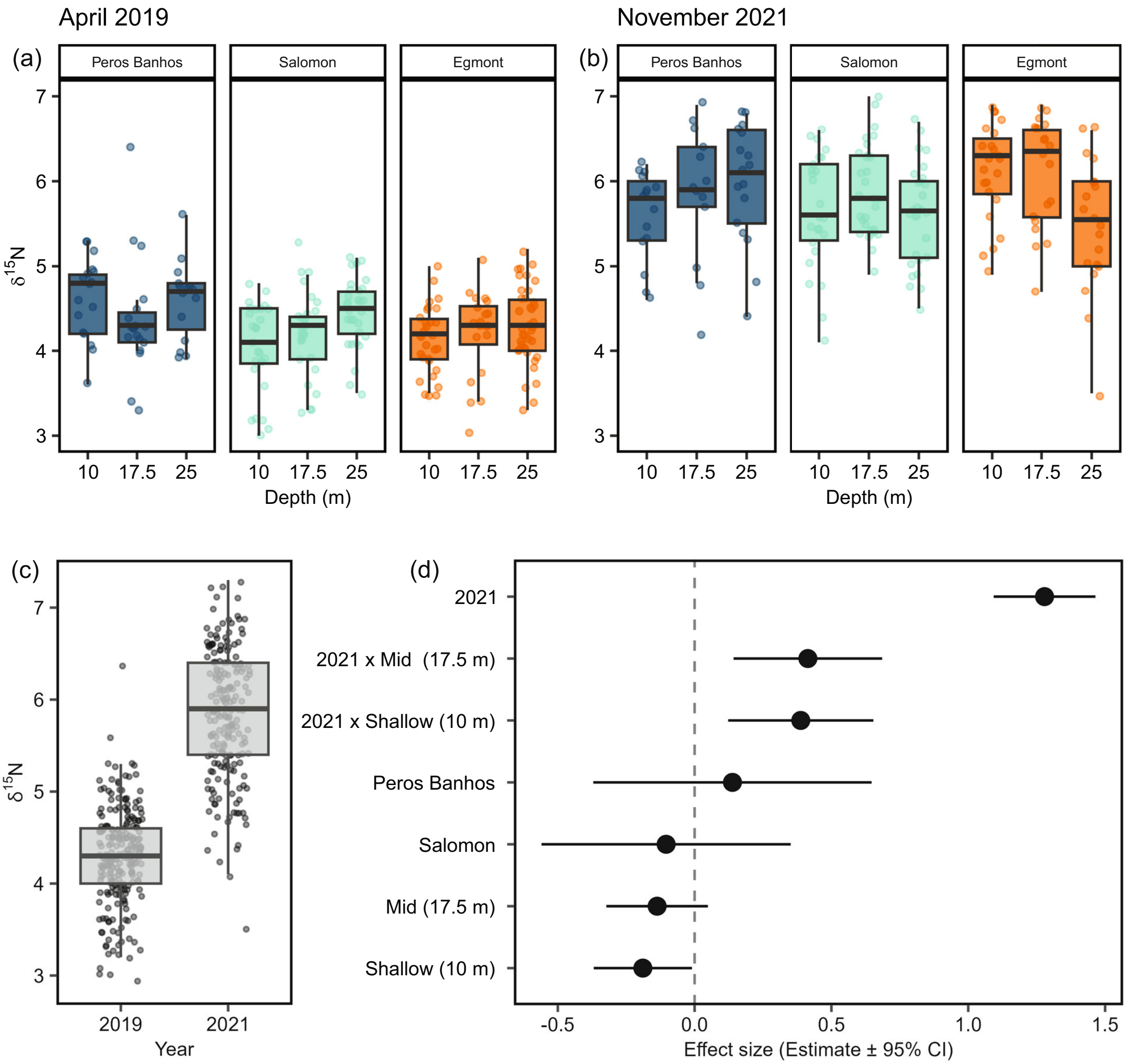

Fig. 6. Interannual variation in *Halimeda* δ^{15}N values across depths (10, 17.5, and 25 m, $n = 10$ replicate samples per site, per depth) on the fore reef slopes around three atolls in the Chagos Archipelago: Peros Banhos Atoll ($n = 2$ sites) and Salomon Atoll ($n = 3$ sites) and Egmont Atoll ($n = 3$ sites) in (**a**) April 2019 and (**b**) November 2021. (**c**) shows total δ^{15}N values for all sites and all depths for each collection year. (**d**) Effect sizes (estimates ± 95% confidence intervals) for the fixed effects of year, depth, and atoll on *Halimeda* δ^{15}N from a linear mixed-effects model, plus the interaction effect between year and depth. Vertical dashed line at zero indicates no effect. Significant effects ($p < 0.05$) occur where confidence intervals do not intersect the vertical dashed line. Enhanced upwelling to shallow reefs is associated with elevated δ^{15}N values in *Halimeda* during 2021.

Pacific. Increased stratification depth between the surface mixed layer and denser water below can impede the upward propagation of deeper, cooler, and nutrient-rich water to shallow reef communities. Across the Chagos Archipelago, we found that a mixed layer depth of greater than ~ 60 m prevents upwelling from occurring at depths of 10–25 m, where reef communities may benefit from the delivery of deep-water nutrients and particulate food subsidies. Conversely, when the mixed layer depth is shallower due to weakened wind velocities, deeper water can more readily move upwards to depths at which shallow reef communities reside. Across the Archipelago, the critical mixed layer depth that results in shallow reef communities experiencing a higher number of Degree Cooling Hours from upwelled water appears to be ~ 40 m (Fig. 3a). Whether the critical depth threshold we identify here applies across reef systems globally remains unknown. A broader application of the analytical approach developed here may help to build a more detailed picture of the cross-scale physical drivers of upwelling dynamics on tropical coral reefs.

We also identified site-level variability in upwelling across the Chagos Archipelago, which was not captured by the site-specific parameters included in our models. We hypothesized that reef slope steepness would affect the upward propagation of deeper water masses up the reef slope; however, we were unable to identify this. This is likely due to the coarse nature of our slope estimates and because we were unable to quantify bathymetry at depths below 70 m, where deeper-water internal waves interacting with bathymetry can drive the upward movement of water masses. The lack of high-resolution bathymetric data on reefs worldwide hinders our ability to resolve variations in upwelling across smaller, site-level scales, which may be important for understanding local differences in internal wave climates.

Power spectral density analyses revealed the primary frequency of oscillation in the temperature time series across all sites at all atolls to be the M2 (twice-daily) lunar tide. This, along with the occurrence of rapid drops in temperature suggestive of the movement of distinct water masses onto the reef slope, indicates that cold pulses across the Archipelago are being driven primarily by internal waves propagating along a density gradient (Leichter et al. 2006). This reinforces the importance of the mixed layer depth—identified in our boosted regression tree models as key to predicting variations in upwelling—as a density boundary along which internal waves may propagate. Where this boundary is shallow, internal waves propagating along the pycnocline can drive cool, nutrient-rich sub-thermocline water to shallow reef communities. Other physical characteristics of the benthic substrate, like reef structural complexity, can also influence water movement (Monismith et al. 2015) and more work is needed to study their interactions and effects on scale-dependent patterns of upwelling on coral reefs. Additionally, we do not here consider the potential impact of mesoscale processes such as eddies, which may be influencing upwelling dynamics at inter-site scales; further research efforts are required to resolve site-level upwelling variability driven by such processes.

The spatial resolution mismatch between reanalysis products (tens of km) and site-level in situ measurements of temperature (tens of meters) makes it challenging to identify the drivers of site-level variations in upwelling. Ultimately, we found that although spatial differences exist that modify upwelling at localized scales, broadly speaking, our analyses indicate that upwelling across the Chagos Archipelago is uniformly driven by large-scale physical processes and closely linked with periodic Indian Ocean Dipole events. The temporal mismatch between daily resolution cumulative Degree Cooling Hours and the monthly resolution predictors included in our model was overcome by building our statistical models in a hierarchical manner, repeating each monthly value over each day in each month. This scale disparity diminishes the likelihood of capturing relationships between these coarse predictors and the finer resolution Degree Cooling Hour response variable. Despite this, the optimal predictor of Degree Cooling Hour variability was the coarser scale monthly resolution estimates of mixed layer depth. This highlights both the ability of the statistical modeling framework to identify relationships across temporally mismatched variables and the strength of the relationship between mixed layer depth and upwelled cold pulses on these shallow reefs.

Long-term climate variability in the Indian Ocean

Our results confirm a strong link between the Indian Ocean Dipole and upwelling variability in the central Indian Ocean. We found that positive dipole phases consistently deepened the surface mixed layer depth over the past 40+ years, each time likely restricting the exposure of shallow reef communities to deeper upwelled water. This was particularly pronounced in 2019, during the strongest positive dipole phase of this century (Shi and Wang 2021). From September to December 2019, at the peak of the dipole event, the mixed layer depth was 113% deeper than the 40-year mean for this period. We recorded a near complete lack of upwelled waters reaching shallow reefs during this time. Total summed Degree Cooling Hours across all three atolls in September and October 2019 were 162% lower than the same period in 2020. During a positive dipole phase, anomalous easterly winds cause the thermocline to shoal in the Eastern Indian Ocean, enhancing upwelling off the coast of Sumatra and driving warm sea-surface temperature anomalies in the Western Indian Ocean (Saji et al. 1999). This ocean–atmosphere feedback, where anomalous easterly winds induce a shoaling thermocline in the Eastern Indian Ocean, driving positive SST anomalies in the west, triggers further atmospheric convection through Bjerknes feedback (Bjerknes 1969). This amplifies positive dipole events in the Indian Ocean (Cai et al. 2013), and is analogous to La Niña in the Pacific. We suggest that during the extreme positive dipole event of 2019, the warm pool of anomalously high sea-surface temperature in the Western Indian Ocean spread out and across the central Indian Ocean, acting to depress the thermocline and increase the depth of the surface mixed layer. This prohibited upwelling reaching shallow reef communities in the region, likely removing a key mechanism of nutrient and particulate food delivery to reef organisms. This strong dipole event caused significant coral bleaching on mesophotic reefs (up to 90 m depth) around Egmont Atoll in the Chagos Archipelago (Diaz et al. 2023), likely due to the unprecedented depth of the thermocline exposing these corals to waters exceeding their ordinary thermal conditions. This observation highlights the importance of mixed layer depth as a physical boundary that can both enhance cooling and resource supply or redistribute stressful conditions (Schramek et al. 2018; Foreman et al. 2024).

Impact on reef biological processes

We show that variations in regional-scale atmospheric and oceanographic drivers directly affect reef-scale biological processes. We observed a temporal shift in the $\delta^{15}N$ values of a common and widely distributed reef macroalga in response to interannual variations in upwelling. Across all three atolls and depths (10, 17.5, and 25 m), $\delta^{15}N$ values of *Halimeda* were enriched in November 2021 compared with April 2019. This increase in $\delta^{15}N$ suggests a different primary source of nitrogen to the benthic community between the two sampling points. The anomalously shallow 16 m mixed layer depth in 2021 suggests favorable upwelling conditions (Fig. 3a), and that enhanced upwelling in November 2021 contributed to the enriched $\delta^{15}N$ values in *Halimeda* across the Chagos Archipelago.

Macroalgae can uptake available nitrogen proportionately to ambient conditions, rather than selectively utilizing ^{14}N as phytoplankton do (Cohen and Fong 2005; Swart et al. 2014). This lack of isotopic fractionation means that macroalgae are a reliable indicator of shifts in the dominant source of nitrogen to a reef system (Leichter et al. 2003; Dailer et al. 2010). Our results suggest that during periods of enhanced upwelling, the shallow reef communities of the Chagos Archipelago are exposed to a distinct source of deep-water nitrogen, which is being assimilated by reef primary producers and likely incorporated into reef food webs. The enriched $\delta^{15}N$ values during the period of greater upwelling are consistent with increased coral and particulate organic matter $\delta^{15}N$ values observed during periods of increased upwelling in the neighboring Maldives Archipelago (Radice et al. 2019). Changes in upwelling can alter the background $\delta^{15}N$ pool, which must be accounted for in community trophic ecology studies, particularly if such studies have a temporal component (de la Vega et al. 2023; Fox et al. 2023).

Future impacts and implications

Upwelling supplies crucial energetic subsidies to shallow reef communities (Leichter et al. 1998, 2003; Aston et al. 2019). However, in a rapidly warming climate, inter- and intra-annual cycles of upwelling are likely to change (Bakun et al. 2015; Wang et al. 2015; Xiu et al. 2018; Abrahams et al. 2021). Climate models predict net nutrient transfer to the deep ocean, increased ocean stratification, and reduced vertical mixing, leading to a drop in surface and subsurface nutrient concentrations and a subsequent reduction in surface ocean primary productivity (Cabré et al. 2015; Fu et al. 2016; Moore et al. 2018). Studies of historical changes in ocean stratification likewise show an increase in stratification in the upper water column over recent decades (Li et al. 2020). For coral reefs in oligotrophic regions, this increased stratification may reduce localized upwelling, leading to a decline in pelagic subsidy delivery and subsequent reduction in primary production.

Given that extreme positive Indian Ocean Dipole events are predicted to increase in frequency in the coming decades (Cai et al. 2013), it is important to understand whether—and to what extent—biological reef communities respond to these dramatic, but short-lived environmental changes. Modeling studies predict a deepening of mixed layer depth in the south equatorial Indian Ocean until 2100 (Gao et al. 2023), which, coupled with the projected increase in conditions resembling positive dipole phases under global warming scenarios, pose the possibility of a markedly different upwelling regime around the Chagos Archipelago over the coming century. To shed light on reef futures, we need to establish how coral reef communities respond to upwelling, and whether gradients in upwelling impact reef resilience to—and recovery from—major disturbance events, such as marine heatwaves and subsequent mass coral bleaching events, that are becoming more frequent under climate change (Hughes et al. 2018).

Author Contributions

Gareth J. Williams and Michael D. Fox conceived of and designed the study, which was then further developed by Danielle L. Spring. The field campaign and data collection were undertaken by Gareth J. Williams, Michael D. Fox, Ronan C. Roche, and John R. Turner. Data curation and analysis was undertaken by Danielle L. Spring, with support from Gareth J. Williams, Michael D. Fox, J. A. Mattias Green, and Robin Guillaume-Castel. Danielle L. Spring wrote the original manuscript draft with Gareth J. Williams, and all authors contributed to reviewing and finalizing the manuscript.

Acknowledgments

The authors thank the United Kingdom Foreign and Commonwealth Office and the British Indian Ocean Territory Administration for allowing us to undertake this research across the Chagos Archipelago under permit. We acknowledge the Bertarelli Foundation for funding administered as part of the Bertarelli Program in Marine Science (Project 6 awarded to John R. Turner, Ronan C. Roche, and Gareth J. Williams at Bangor University). We further acknowledge support provided by KAUST Baseline Research Funding to Michael D. Fox, and Brian Wilson for purchasing additional temperature loggers. We thank Daniel Bayley, Kathryn Dawson, Andrew Mogg, and the crew of the Grampian Frontier for their assistance in conducting fieldwork. Finally, we thank Ade Fewings and Oliver Barbaresi for their technical programming support.

Conflicts of Interest

The authors declare no conflict of interest.

Data Availability Statement

The data and statistical scripts that support the findings of this study are available on GitHub (https://github.com/daniellelucyspring/Upwelling-drivers).

References

Abrahams, A., R. W. Schlegel, and A. J. Smit. 2021. "Variation and Change of Upwelling Dynamics Detected in the World's Eastern Boundary Upwelling Systems." *Frontiers in Marine Science* 8: 626411. https://doi.org/10.3389/FMARS.2021.626411/BIBTEX.

Aston, E. A., G. J. Williams, J. A. M. Green, et al. 2019. "Scale-Dependent Spatial Patterns in Benthic Communities Around a Tropical Island Seascape." *Ecography* 42, no. 3: 578–590. https://doi.org/10.1111/ECOG.04097.

Bakun, A. 1990. "Global Climate Change and Intensification of Coastal Ocean Upwelling." *Science* 247, no. 4939: 198–201. https://doi.org/10.1126/SCIENCE.247.4939.198.

Bakun, A., B. Black, S. Bograd, et al. 2015. "Anticipated Effects of Climate Change on Coastal Upwelling Ecosystems." *Current Climate Change Reports* 1, no. 2: 85–93. https://doi.org/10.1007/S40641-015-0008-4/FIGURES/2.

Bakun, A., D. B. Field, A. Redondo-Rodriguez, and S. J. Weeks. 2010. "Greenhouse Gas, Upwelling-Favorable Winds, and the Future of Coastal Ocean Upwelling Ecosystems." *Global Change Biology* 16, no. 4: 1213–1228. https://doi.org/10.1111/J.1365-2486.2009.02094.X.

Becker, D. M., H. M. Putnam, D. E. Burkepile, T. C. Adam, R. Vega Thurber, and N. J. Silbiger. 2021. "Chronic Low-Level Nutrient Enrichment Benefits Coral Thermal Performance in a Fore Reef Habitat." *Coral Reefs* 40, no. 5: 1637–1655. https://doi.org/10.1007/s00338-021-02138-2.

Behringer, D., and Y. Xue. 2004. "Evaluation of the Global Ocean Data Assimilation System at NCEP: The Pacific Ocean." In Proceedings of the Eighth Symposium on Integrated Observing and Assimilation Systems for Atmosphere, Oceans, and Land Surface, AMS 84th Annual Meeting, Washington State Convention and Trade Center.

Bjerknes, J. 1969. "Atmospheric Teleconnections From the Equatorial Pacific." *Monthly Weather Review* 97, no. 3: 163–172. https://doi.org/10.1175/1520-0493(1969)097%3C0163:ATFTEP%3E2.3.CO;2.

Breiman, L. 2011. "Statistical Modeling: The Two Cultures." *Statistical Science* 16, no. 3: 199–215. http://www2.math.uu.se/~thulin/mm/breiman.pdf.

Cabré, A., I. Marinov, and S. Leung. 2015. "Consistent Global Responses of Marine Ecosystems to Future Climate Change across the IPCC AR5 Earth System Models." *Climate Dynamics* 45: 1253–1280. https://doi.org/10.1007/s00382-014-2374-3.

Cai, W., A. Sullivan, and T. Cowan. 2009. "Climate Change Contributes to More Frequent Consecutive Positive Indian Ocean Dipole Events." *Geophysical Research Letters* 36, no. 23: 1–5. https://doi.org/10.1029/2009GL040163.

Cai, W., X. T. Zheng, E. Weller, et al. 2013. "Projected Response of the Indian Ocean Dipole to Greenhouse Warming." *Nature Geoscience* 6, no. 12: 999–1007. https://doi.org/10.1038/ngeo2009.

Carr, M. E. 2001. "Estimation of Potential Productivity in Eastern Boundary Currents Using Remote Sensing." *Deep-Sea Research Part II: Topical Studies in Oceanography* 49, no. 1–3: 59–80. https://doi.org/10.1016/S0967-0645(01)00094-7.

Cohen, R. A., and P. Fong. 2005. "Experimental Evidence Supports the Use of $\delta^{15}N$ Content of the Opportunistic Green Macroalga *Enteromorpha intestinalis* (Chlorophyta) to Determine Nitrogen Sources to Estuaries." *Journal of Phycology* 41, no. 2: 287–293. https://doi.org/10.1111/j.1529-8817.2005.04022.x.

Cushing, D. H. 1989. "A Difference in Structure Between Ecosystems in Strongly Stratified Waters and in Those That Are Only Weakly Stratified." *Journal of Plankton Research* 11, no. 1: 1–13. https://doi.org/10.1093/plankt/11.1.1.

Dailer, M. L., R. S. Knox, J. E. Smith, M. Napier, and C. M. Smith. 2010. "Using $\delta^{15}N$ Values in Algal Tissue to Map Locations and Potential Sources of Anthropogenic Nutrient Inputs on the Island of Maui, Hawai'i, USA." *Marine Pollution Bulletin* 60, no. 5: 655–671. https://doi.org/10.1016/j.marpolbul.2009.12.021.

Davis, K. A., R. S. Arthur, E. C. Reid, et al. 2020. "Fate of Internal Waves on a Shallow Shelf." *Journal of Geophysical Research: Oceans* 125, no. 5: 1–18. https://doi.org/10.1029/2019JC015377.

de la Vega, C., J. Kershaw, G. B. Stenson, et al. 2023. "Multi-Decadal Trends in Biomarkers in Harp Seal Teeth From the North Atlantic Reveal the Influence of Prey Availability on Seal Trophic Position." *Global Change Biology* 29, no. 19: 5582–5595. https://doi.org/10.1111/gcb.16889.

DeCarlo, T. M., L. Gajdzik, J. Ellis, et al. 2020. "Nutrient-Supplying Ocean Currents Modulate Coral Bleaching Susceptibility." *Science Advances* 6, no. 34: 1–7. https://doi.org/10.1126/sciadv.abc5493.

DeCarlo, T. M., S. Carvalho, L. Gajdzik, et al. 2021. "Patterns, Drivers, and Ecological Implications of Upwelling in Coral Reef Habitats of the Southern Red Sea." *Journal of Geophysical Research: Oceans* 126, no. 2: e2020JC016493. https://doi.org/10.1029/2020JC016493.

Diaz, C., N. L. Foster, M. J. Attrill, et al. 2023. "Mesophotic Coral Bleaching Associated With Changes in Thermocline Depth." *Nature Communications* 14, no. 1: 6528. https://doi.org/10.1038/s41467-023-42279-2.

Eidens, C., E. Bayraktarov, T. Hauffe, V. Pizarro, T. Wilke, and C. Wild. 2014. "Benthic Primary Production in an Upwelling-Influenced Coral Reef, Colombian Caribbean." *PeerJ* 2, no. 1: e554. https://doi.org/10.7717/PEERJ.554.

Elith, J., J. R. Leathwick, and T. Hastie. 2008. "A Working Guide to Boosted Regression Trees." *Journal of Animal Ecology* 77, no. 4: 802–813. https://doi.org/10.1111/j.1365-2656.2008.01390.x.

Fiedler, P. C. 2010. "Comparison of Objective Descriptions of the Thermocline." *Limnology and Oceanography: Methods* 8, no. 6: 313–325. https://doi.org/10.4319/LOM.2010.8.313.

Foreman, A. D., N. N. Duprey, M. Yuval, et al. 2024. "Severe Cold-Water Bleaching of a Deep-Water Reef Underscores Future Challenges for Mesophotic Coral Ecosystems." *Science of the Total Environment* 951, no. July: 175210. https://doi.org/10.1016/j.scitotenv.2024.175210.

Fox, M. D., G. J. Williams, M. D. Johnson, et al. 2018. "Gradients in Primary Production Predict Trophic Strategies of Mixotrophic Corals Across Spatial Scales." *Current Biology* 28, no. 21: 3355–3363.e4. https://doi.org/10.1016/J.CUB.2018.08.057.

Fox, M. D., R. Guillaume-Castel, C. B. Edwards, et al. 2023. "Ocean Currents Magnify Upwelling and Deliver Nutritional Subsidies to Reef-Building Corals During El Niño Heatwaves." *Science Advances* 9, no. 24: eadd5032. https://doi.org/10.1126/sciadv.add5032.

Friedman, J. H., and J. J. Meulman. 2003. "Multiple Additive Regression Trees With Application in Epidemiology." *Statistics in Medicine* 22, no. 9: 1365–1381. https://doi.org/10.1002/sim.1501.

Fu, W., J. T. Randerson, and J. K. Moore. 2016. "Climate Change Impacts on Net Primary Production (NPP) and Export Production (EP) Regulated by Increasing Stratification and Phytoplankton Community Structure in the CMIP5 Models." *Biogeosciences* 13, no. 18: 5151–5170. https://doi.org/10.5194/BG-13-5151-2016.

Gao, Z., S.-M. Long, J.-R. Shi, L. Cheng, G. Li, and J. Ying. 2023. "Indian Ocean Mixed Layer Depth Changes Under Global Warming." *Frontiers in Climate* 5: 1112713. https://doi.org/10.3389/FCLIM.2023.1112713.

Gove, J. M., M. A. McManus, A. B. Neuheimer, et al. 2016. "Near-Island Biological Hotspots in Barren Ocean Basins." *National Geographic Society* 7: 1–17. https://doi.org/10.1038/ncomms10581.

Gove, J. M., M. A. Merrifield, and R. E. Brainard. 2006. "Temporal Variability of Current-Driven Upwelling at Jarvis Island." *Journal of Geophysical Research: Oceans* 111, no. C12: 12011. https://doi.org/10.1029/2005JC003161.

Guillaume-Castel, R., G. J. Williams, J. S. Rogers, J. M. Gove, and J. A. M. Green. 2021. "Quantifying Upwelling in Tropical Shallow Waters: A Novel Method Using a Temperature Stratification Index." *Limnology and Oceanography: Methods* 19: 566–577. https://doi.org/10.1002/lom3.10449.

Hays, G. C., H. J. Koldewey, S. Andrzejaczek, et al. 2020. "A Review of a Decade of Lessons From One of the World's Largest MPAs: Conservation Gains and Key Challenges." *Marine Biology* 167, no. 11: 1–22. https://doi.org/10.1007/S00227-020-03776-W.

Hijmans, R. J., and J. Elith. 2017. Species Distribution Modeling With R Cran Project.

Hughes, T. P., K. D. Anderson, S. R. Connolly, et al. 2018. "Spatial and Temporal Patterns of Mass Bleaching of Corals in the Anthropocene." *Science* 359, no. 6371: 80–83. https://doi.org/10.1126/science.aan8048.

Hughes, T. P., M. L. Barnes, D. R. Bellwood, et al. 2017. "Coral Reefs in the Anthropocene." *Nature* 546, no. 7656: 82–90. https://doi.org/10.1038/nature22901.

Jantzen, C., G. M. Schmidt, C. Wild, C. Roder, S. Khokiattiwong, and C. Richter. 2013. "Benthic Reef Primary Production in Response to Large Amplitude Internal Waves at the Similan Islands (Andaman Sea, Thailand)." *PLoS One* 8, no. 11: e81834. https://doi.org/10.1371/journal.pone.0081834.

Johnson, M. D., J. J. Scott, M. Leray, et al. 2021. "Rapid Ecosystem-Scale Consequences of Acute Deoxygenation on a Caribbean Coral Reef." *Nature Communications* 12, no. 1: 1–12. https://doi.org/10.1038/s41467-021-24777-3.

Johnson, M. D., M. D. Fox, E. L. A. Kelly, et al. 2020. "Ecophysiology of Coral Reef Primary Producers Across an Upwelling Gradient in the Tropical Central Pacific." *PLOS ONE* 15, no. 2: e0228448. https://doi.org/10.1371/JOURNAL.PONE.0228448.

Jouffray, J. B., L. M. Wedding, A. V. Norström, et al. 2019. "Parsing Human and Biophysical Drivers of Coral Reef Regimes." *Proceedings of the Royal Society B: Biological Sciences* 286, no. 1896: 1–10. https://doi.org/10.1098/rspb.2018.2544.

Leichter, J. J., and S. J. Genovese. 2006. "Intermittent Upwelling and Subsidized Growth of the Scleractinian Coral Madracis Mirabilis on the Deep Fore-Reef Slope of Discovery Bay, Jamaica." *Marine Ecology Progress Series* 316, no. 2003: 95–103. https://doi.org/10.3354/meps316095.

Leichter, J. J., B. Helmuth, and A. M. Fischer. 2006. "Variation Beneath the Surface: Quantifying Complex Thermal Environments on Coral Reefs in the Caribbean, Bahamas and Florida." *Journal of Marine Research* 64, no. 4: 563–588. https://doi.org/10.1357/002224006778715711.

Leichter, J. J., G. Shellenbarger, S. J. Genovese, and S. R. Wing. 1998. "Breaking Internal Waves on a Florida (USA) Coral Reef: A Plankton Pump at Work?" *Marine Ecology Progress Series* 166: 83–97. https://doi.org/10.3354/MEPS166083.

Leichter, J. J., H. L. Stewart, and S. L. Miller. 2003. "Episodic Nutrient Transport to Florida Coral Reefs." *Limnology and Oceanography* 48, no. 4: 1394–1407. https://doi.org/10.4319/lo.2003.48.4.1394.

Leichter, J. J., M. D. Stokes, J. L. Hench, J. Witting, and L. Washburn. 2012. "The Island-Scale Internal Wave Climate of Moorea, French Polynesia." *Journal of Geophysical Research* 117: 6008. https://doi.org/10.1029/2012JC007949.

Leichter, J. J., S. R. Wing, S. L. Miller, and M. W. Denny. 1996. "Pulsed Delivery of Subthermocline Water to Conch Reef (Florida Keys) by Internal Tidal Bores." *Limnology and*

Oceanography 41, no. 7: 1490–1501. https://doi.org/10.4319/LO.1996.41.7.1490.

Li, G., L. Cheng, J. Zhu, et al. 2020. "Increasing Ocean Stratification Over the Past Half-Century." *Nature Climate Change* 10, no. 12: 1116–1123. https://doi.org/10.1038/s41558-020-00918-2.

Lowe, R. J., and J. L. Falter. 2015. "Oceanic Forcing of Coral Reefs." *Annual Review of Marine Science* 7: 43–66. https://doi.org/10.1146/annurev-marine-010814-015834.

Marangoni, L. F. D., C. Rottier, and C. Ferrier-Pagès. 2021. "Symbiont Regulation in *Stylophora pistillata* During Cold Stress: An Acclimation Mechanism against Oxidative Stress and Severe Bleaching." *Journal of Experimental Biology* 224, no. 3: 1–10. https://doi.org/10.1242/jeb.235275.

Miller, S. D., B. J. Zgliczynski, M. D. Fox, et al. 2019. "Niche Width Expansion of Coral Reef Fishes Along a Primary Production Gradient in the Remote Central Pacific." *Marine Ecology Progress Series* 625: 127–143. https://doi.org/10.3354/meps13023.

Monismith, S. G., J. S. Rogers, D. Koweek, and R. B. Dunbar. 2015. "Frictional Wave Dissipation on a Remarkably Rough Reef." *Geophysical Research Letters* 42: 4063–4071. https://doi.org/10.1002/2015GL063804.

Moore, J. K., W. Fu, F. Primeau, et al. 2018. "Sustained Climate Warming Drives Declining Marine Biological Productivity." *Science* 359, no. 6380: 113–1143. https://doi.org/10.1126/science.aao6379.

Morais, R. A., and D. R. Bellwood. 2019. "Pelagic Subsidies Underpin Fish Productivity on a Degraded Coral Reef." *Current Biology* 29, no. 9: 1521–1527.e6. https://doi.org/10.1016/j.cub.2019.03.044.

Müller, D., P. J. Leitão, and T. Sikor. 2013. "Comparing the Determinants of Cropland Abandonment in Albania and Romania Using Boosted Regression Trees." *Agricultural Systems* 117: 66–77. https://doi.org/10.1016/j.agsy.2012.12.010.

Pauly, D., and V. Christensen. 1995. "Primary Production Required to Sustain Global Fisheries." *Nature* 374: 255–257. https://doi.org/10.1038/374255a0.

Pugh, D. T., and R. F. Rayner. 1981. "The Tidal Regimes of Three Indian Ocean Atolls and some Ecological Implications." *Estuarine, Coastal and Shelf Science* 13, no. 4: 389–407. https://doi.org/10.1016/S0302-3524(81)80036-9.

R Core Team, R: A language and environment for statistical computing. 2020.

Radice, V. Z., O. Hoegh-Guldberg, B. Fry, M. D. Fox, and S. G. Dove. 2019. "Upwelling as the Major Source of Nitrogen for Shallow and Deep Reef-Building Corals across an Oceanic Atoll System." *Functional Ecology* 33, no. 6: 1120–1134. https://doi.org/10.1111/1365-2435.13314.

Randall, C. J., L. T. Toth, J. J. Leichter, J. L. Maté, and R. B. Aronson. 2019. "Upwelling Buffers Climate Change Impacts on Coral Reefs of the Eastern Tropical Pacific." *Ecology* 101, no. 2: e02918. https://doi.org/10.1002/ecy.2918.

Rebert, J. P., J. R. Donguy, G. Eldin, and K. Wyrtki. 1985. "Relations Between Sea Level, Thermocline Depth, Heat Content, and Dynamic Height in the Tropical Pacific Ocean." *Journal of Geophysical Research* 90, no. C6: 11719–11725. https://doi.org/10.1029/jc090ic06p11719.

Reid, E. C., T. M. DeCarlo, A. L. Cohen, et al. 2019. "Internal Waves Influence the Thermal and Nutrient Environment on a Shallow Coral Reef." *Limnology and Oceanography* 64, no. 5: 1949–1965. https://doi.org/10.1002/lno.11162.

Saji, N. H., B. N. Goswami, P. N. Vinayachandran, and T. Yamagata. 1999. "A Dipole Mode in the Tropical Indian Ocean." *Nature* 401, no. 6751: 360–363. https://doi.org/10.1038/43854.

Schmidt, G. M., M. Wall, M. Taylor, C. Jantzen, and C. Richter. 2016. "Large-Amplitude Internal Waves Sustain Coral Health During Thermal Stress." *Coral Reefs* 35, no. 3: 869–881. https://doi.org/10.1007/s00338-016-1450-z.

Schott, F. A., and J. P. McCreary. 2001. "The Monsoon Circulation of the Indian Ocean." *Progress in Oceanography* 51, no. 1: 1–123. https://doi.org/10.1016/S0079-6611(01)00083-0.

Schramek, T. A., P. L. Colin, M. A. Merrifield, and E. J. Terrill. 2018. "Depth-Dependent Thermal Stress Around Corals in the Tropical Pacific Ocean." *Geophysical Research Letters* 45, no. 18: 9739–9747. https://doi.org/10.1029/2018GL078782.

Shi, W., and M. Wang. 2021. "A Biological Indian Ocean Dipole Event in 2019." *Scientific Reports* 11, no. 1: 1–8. https://doi.org/10.1038/s41598-021-81410-5.

Spring, D. L., and G. J. Williams. 2023. "Influence of Upwelling on Coral Reef Benthic Communities: A Systematic Review and Meta-Analysis." *Proceedings of the Royal Society B* 290: 20230023. https://doi.org/10.1098/rspb.2023.0023.

Stuhldreier, I., I. Stuhldreier, S. Celeste, et al. 2015. "Upwelling Increases Net Primary Production of Corals and Reef-Wide Gross Primary Production Along the Pacific Coast of Costa Rica." *Frontiers in Marine Science* 2: 1–14. https://doi.org/10.3389/fmars.2015.00113.

Sturaro, N., Y. E. Hsieh, Q. Chen, P. L. Wang, and V. Denis. 2021. "Trophic Plasticity of Mixotrophic Corals Under Contrasting Environments." *Functional Ecology* 35: 2841–2855. https://doi.org/10.1111/1365-2435.13924.

Swart, P. K., S. Evans, T. Capo, and M. A. Altabet. 2014. "The Fractionation of Nitrogen and Oxygen Isotopes in Macroalgae During the Assimilation of Nitrate." *Biogeosciences* 11, no. 21: 6147–6157. https://doi.org/10.5194/bg-11-6147-2014.

Tkachenko, K. S., and K. Soong. 2017. "Dongsha Atoll: A Potential Thermal Refuge for Reef-Building Corals in the South China Sea." *Marine Environmental Research* 127: 112–125. https://doi.org/10.1016/j.marenvres.2017.04.003.

Vroom, P. S., C. M. Smith, J. A. Coyer, et al. 2003. "Field Biology of Halimeda Tuna (Bryopsidales, Chlorophyta) Across a

Depth Gradient: Comparative Growth, Survivorship, Recruitment, and Reproduction." *Hydrobiologia* 501: 149–166. https://doi.org/10.1023/A:1026287816324.

Wall, M., L. Putchim, G. M. Schmidt, C. Jantzen, S. Khokiattiwong, and C. Richter. 2015. "Large-Amplitude Internal Waves Benefit Corals During Thermal Stress." *Proceedings of the Royal Society B: Biological Sciences* 282, no. 1799: 20140650. https://doi.org/10.1098/RSPB.2014.0650.

Wang, D., T. C. Gouhier, B. A. Menge, and A. R. Ganguly. 2015. "Intensification and Spatial Homogenization of Coastal Upwelling Under Climate Change." *Nature* 518, no. 7539: 390–394. https://doi.org/10.1038/nature14235.

Wang, L. C., T. L. Dao, and J. Y. Yu. 2022. "Continued Weakening of the Equatorial Pacific Upwelling Annual Cycle in CMIP5 Future Projections." *Scientific Reports* 12, no. 1: 1–12. https://doi.org/10.1038/s41598-022-19874-2.

Welch, P. D. 1967. "The Use of Fast Fourier Transform for the Estimation of Power Spectra: A Method Based on Time Aver. Aging Over Short, Modified Periodograms." *IEEE Transactions on Audio and Electroacoustics* 15, no. 2: 70–73.

Williams, G. J., and N. A. J. Graham. 2019. "Rethinking Coral Reef Functional Futures." *Functional Ecology* 33: 942–947. https://doi.org/10.1111/1365-2435.13374.

Williams, G. J., S. A. Sandin, B. J. Zgliczynski, et al. 2018. "Biophysical Drivers of Coral Trophic Depth Zonation." *Marine Biology* 165, no. 4: 1–15. https://doi.org/10.1007/S00227-018-3314-2/FIGURES/5.

Wolanski, E., E. Drew, K. M. Abel, and J. O'Brien. 1988. "Tidal Jets, Nutrient Upwelling and Their Influence on the Productivity of the Alga Halimeda in the Ribbon Reefs, Great Barrier Reef." *Estuarine, Coastal and Shelf Science* 26, no. 2: 169–201. https://doi.org/10.1016/0272-7714(88)90049-2.

Wyatt, A. S. J., J. J. Leichter, L. T. Toth, T. Miyajima, R. B. Aronson, and T. Nagata. 2020. "Heat Accumulation on Coral Reefs Mitigated by Internal Waves." *Nature Geoscience* 13, no. 1: 28–34. https://doi.org/10.1038/s41561-019-0486-4.

Wyatt, A. S. J., J. J. Leichter, L. Washburn, L. Kui, P. J. Edmunds, and S. C. Burgess. 2023. "Hidden Heatwaves and Severe Coral Bleaching Linked to Mesoscale Eddies and Thermocline Dynamics." *Nature Communications* 14, no. 1: 1–17. https://doi.org/10.1038/s41467-022-35550-5.

Xiu, P., F. Chai, E. N. Curchitser, and F. S. Castruccio. 2018. "Future Changes in Coastal Upwelling Ecosystems With Global Warming: The Case of the California Current System." *Scientific Reports* 8, no. 1: 1–9. https://doi.org/10.1038/s41598-018-21247-7.

Xu, X., L. Wang, and W. Yu. 2021. "The Unique Mean Seasonal Cycle in the Indian Ocean Anchors Its Various Air–Sea Coupled Modes Across the Basin." *Scientific Reports* 11, no. 1: 1–8. https://doi.org/10.1038/s41598-021-84936-w.

Supporting Information

Additional Supporting Information may be found in the online version of this article.

Submitted 16 September 2024
Revised 15 April 2025
Accepted 30 July 2025