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Large-scale effects of turbidity on coral bleaching in the Hawaiian islands

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Turbidity from land-based runoff has been identified as a possible driver of
coral bleaching refugia, as particulate matter in turbid habitats may block
excessive irradiance and alter the food supply to corals during ocean
heatwaves. However, negative effects of turbidity have also been
documented worldwide, and high-resolution data across reef regions are
required to identify habitats where turbidity is harmful or helpful during
heatwaves. We monitored turbidity across five Main Hawaiian Islands during
a 2019 ocean heatwave using Planet Dove satellites (3.7 m spatial resolution,
extracted at 100 m resolution) to examine relationships between turbidity and
coral bleaching occurrence and severity. We also attributed turbidity to urban
and non-urban land uses to determine how turbidity associated with different
human activities affects coral bleaching. We found that, while turbidity had a
negative relationship with coral bleaching severity, this effect weakened at
higher temperatures, especially in rural areas. However, turbidity maintained a
slightly negative effect on bleaching severity in urban settings. In addition, while
thermal stress was the predominant driver of bleaching occurrence,
interactions between temperature and local variables like turbidity and wave
energy were the most significant drivers of bleaching severity. This study
represents one of the first high-resolution analyses of turbid refugia at large
spatial scales. We show how new data sources from remote sensing can
provide scalable yet context-specific information to coastal managers
addressing land-sea runoff.

Introduction

Coral reefs are experiencing increased bleaching events worldwide, jeopardizing marine biodiversity, coastal infrastructure, and livelihoods in fishing and tourism (Burke et al., 2011; Osborne et al., 2017; Hughes et al., 2018). As ocean heatwaves intensify, additional research is needed to identify areas where corals can survive thermal stress. At the land-sea interface, nearshore runoff has been identified as a possible driver of coral refugia (Camp et al., 2018; Sully and van Woesik, 2020). The deposition of soils, sewage, and other particulate and dissolved matter from land to sea can alter water properties and impact coral bleaching in several important ways. First, suspended sediment may serve as a sunshade for light entering the water column, reducing ultraviolet light exposure and photoinhibition of corals during bleaching events (Morgan et al., 2017). In addition, turbidity is an indicator of dissolved organic matter, particulate organic matter, and zooplankton in the water column, which can provide corals with an alternative, heterotrophic pool of fixed carbon during bleaching events, compensating for their loss of photosynthesis (Grottoli et al., 2006; Anthony et al., 2007; Houlbrèque and Ferrier-Pagès, 2009). Given that turbidity has long been considered a coastal pollutant associated with sediment deposition and coral degradation from smothering, light limitation, water chemistry alterations, and other effects, further research is needed to determine if and where enabling conditions for refugia occur.

Numerous studies provide early evidence of turbidity effects on coral bleaching. A recent case study on the Great Barrier Reef found low bleaching in one turbid reef relative to regional bleaching means (Morgan et al., 2017). In a global study of turbidity patterns, Sully and van Woesik (2020) found that regions with remotely sensed turbidity of 0.080-0.127 K_d490 (attenuation coefficient at 490 nanometers observed from satellite sensors) underwent less bleaching during thermal events than areas with minimal turbidity. Cacciapaglia and van Woesik (2016) likewise estimated that turbidity offsets bleaching in 9% of reef habitat threatened by ocean warming in the Indian and Pacific Oceans. In the Florida Keys, reefs in turbid, inshore waters exhibited higher coral cover, higher growth rates, and lower partial mortality rates than offshore reefs (Lirman and Fong, 2007). A bleaching survey in Palau showed lower bleaching incidence inshore compared to offshore, perhaps due to coral shading from land-based runoff inshore (van Woesik et al., 2012); however, this study treated coral proximity to shore as a proxy for turbidity, and other confounding variables may protect corals from bleaching nearshore such as variable temperature at shallow depths (Safaie et al., 2018).

There is disagreement on the effects of turbidity, with some case studies and experiments showing severe bleaching in highly sedimented reefs. Surveys in northwestern Australia and Okinawa Island, Japan demonstrated steep declines in coral cover due to thermal stress on nearshore reefs with heavy runoff (Hongo and Yamano, 2013; Lafratta et al., 2017). On Palmyra Atoll, turbidity was the strongest predictor of bleaching across all taxa, outweighing thermal anomalies (Williams et al. (2010). Paling and bleaching has also been observed in corals exposed to low light under realistic dredging conditions (<0.1 mol photons m^{-2} d^{-1} for 10 d) (Bessell-Browne et al., 2017a). Sediment deposition after bleaching (e.g., from dredging) may exacerbate mortality, as corals have reduced sediment-rejection ability after thermal stress (Bessell-Browne et al., 2017c), and sediment cleaning and/or low light can also reduce coral lipid stores needed to survive bleaching (Fisher et al., 2019). Sediment may also inhibit heterotrophy if excessive sediment causes polyps to retract or otherwise reject particulates (Mills and Sebens, 1997; Anthony, 2000; Jones et al., 2016). In addition, the nutritive benefits of turbidity during bleaching may be limited to certain species like *Montipora capitata* and *Goniastrea retiformis*, which show higher heterotrophy than *Porites compressa* in tank experiments (Grottoli et al., 2006), and heterotrophy may decline with repeat bleaching (Levas et al., 2016).

Suspended sediment is a known driver of reef degradation. Effects of suspended sediments include, but are not limited to, polyp smothering, excessive light limitation, increased coral competitors like macroalgae and filter feeders, and changes in the oxygenation and chemical environment of corals (Fabricius, 2005; Brodie et al., 2012; Jones et al., 2016; Jones et al., 2020; Carlson et al., 2021). Foliose and encrusting corals may be more susceptible to sediment smothering than other, branching species (Jones et al., 2019) as depressions in the colony structure accumulate sediment, and pocilloporid species are sensitive to low light conditions (Jones et al., 2020a; Luter et al., 2021). Sediment may also induce a suite of coral reproductive impairments including disruption of light-based spawning cues, failed surface ascension of egg-sperm bundles due to sediment blocking, reduced coral recruitment, and increased post-settlement mortality (Jones et al., 2015; Brunner et al., 2022). Recent studies indicate that light reduction, relative to sediment itself, is a strong driver of coral loss; in one experiment, corals treated with suspended sediment absent light mitigation displayed no significant change, whereas corals treated with low light exhibited decreased chlorophyll *a* and increased bleaching (Bessell-Browne et al., 2017b). In addition, turbidity often covaries with high nitrate input, which has been found to exacerbate bleaching severity at low levels of temperature stress (Fabricius, 2005; Donovan et al., 2020).

Inconsistencies among past studies on turbidity effects may also arise from inconsistent sources of turbidity, which is a light-based rather than biochemical metric. Turbidity can arise from multiple sources, ranging from dissolved organic matter to silt and marine snow. Particulate matter varies by grain size, color,

organic content, and other properties which could have differential impacts on corals. For example, Storlazzi et al. (2015) found that light attenuation is highest when sediment has a fine grain size and darker color; however, fine sediment is also most persistent and likely to create a "light rain" of particles in the water column that is harmful to corals (Erftemeijer et al., 2012). Turbidity may be comprised of different fractions of dissolved organic matter, detrital particulate organic matter, zooplankton, phytoplankton, and pico- or nano-plankton, which provide variable food quality to corals (Ferrier, 1991; Hoegh-Guldberg and Williamson, 1999; Houlbrèque and Ferrier-Pagès, 2009). For example, pico- and nano-plankton provide three times more nitrogen to *Stylophora pistillata*, relative to dissolved nitrogen (Grover et al., 2002, 2003), and corals have shown preferential feeding on zooplankton in tank experiments (Palardy et al., 2008). Finally, turbidity may be associated with different levels of toxins, where agrochemicals (fertilizers, pesticides, herbicides) are more likely to originate from rural areas and golf courses, and petroleum and medical waste from urban areas. Urban environments can give rise to distinctive "marginal reefs" where corals display unique species assemblages, habitat preferences, reproductive strategies, heterotrophic behavior, and bleaching response, perhaps reflecting specific interactions between urban runoff and local taxa (Camp et al., 2018; Heery et al., 2018).

Past research has been limited in scale, based primarily on case studies that may not represent coral reefs in other regions. A few, global studies have used NASA MODerate-resolution Imaging Spectroradiometer (MODIS) Aqua satellite data to measure the link between turbidity and bleaching (Cacciapaglia and van Woesik, 2016; Sully and van Woesik, 2020); however, these data are too coarse (4 km resolution) to capture many shallow, nearshore features that carry turbidity onto reefs, particularly as 4 km pixels overlapping the coast contain signal from both ocean and land and therefore cannot be used to detect turbidity. In fact, 4 km represents the maximum transport edge for very fine sediment (maximum 3-5 km offshore in previous literature) (Bartley et al., 2014), and this resolution is likely inadequate to characterize variable coastal flux. As a result of these limitations, past studies have not compared different sources of turbidity to determine if certain types of turbidity are more favorable to corals in terms of bleaching than others. Coastal managers require a more detailed understanding of potential turbid refugia in order to address harmful and helpful sources of runoff.

We addressed these gaps by using turbidity data extracted from high-resolution Planet Dove satellite imagery (3.7 m source imagery extracted at 100 m) to measure the effect of turbidity on coral bleaching during a moderate bleaching event in the Hawaiian Islands. We also investigated whether turbidity from predominantly urban versus undeveloped/rural areas have a differential effect on coral bleaching. We applied an algorithm specifically designed to track turbidity in shallow, nearshore waters (Li et al., 2022), demonstrating how advances in the

spatial and temporal resolution of satellite data can help managers access actionable information.

Materials and methods

The Hawaiian archipelago is the longest contiguous island chain in the world, arising from periodic volcanic activity on the Pacific lithospheric plate over the past 27.7 million years (Juvik and Juvik, 1998). Due in part to stratification in volcanic substrate, Hawai'i represents a "model ecosystem" where a range of habitat conditions can be studied across a relatively small area (Vitousek, 1995). Coral reefs in Hawai'i exist along gradients of temperature, solar radiation, nutrients, oceanography, substrate ages, bathymetry, and wind and wave shelter (Grigg, 1983) and experience variable human development and access. Hawai'i therefore offers an opportune context for comparing coral health across taxonomic, light, and turbidity regimes, in waters marked by different levels of human sewage and volcanic silt.

We compared remotely sensed turbidity to coral bleaching occurrence (presence/absence of bleaching) and severity (% bleached of live coral cover) across five Main Hawaiian Islands (Hawai'i, Maui, O'ahu, Lāna'i, Moloka'i) during a prolonged heat stress event from August through December 2019. During this event, sea-surface temperature anomalies (SSTa) exceeded 2 degrees Celsius and SST surpassed 29 degrees Celsius (Figure 1), causing mild to severe bleaching in over 50% of corals statewide (Winston et al., 2020).

Coral surveys

Data from 1,024 bleaching surveys across the Main Hawaiian Islands were obtained from the Hawai'i Coral Bleaching Collaborative (Hawai'i Coral Bleaching Collaborative, 2021), a monitoring partnership created in response to the 2019 Hawai'i coral bleaching event and comprised of NOAA Fisheries Ecosystem Sciences Division; State of Hawai'i Department of Land and Natural Resources, Division of Aquatic Resources; Scripps Institution of Oceanography; Arizona State University; National Park Service, Pacific Island Inventory & Monitoring Network; Hawai'i Institute of Marine Biology; and The Nature Conservancy of Hawai'i. Survey and site selection methods differed slightly across organizations, and thus we included organization as a random factor in our analysis (see "Data Analysis" below). Coral bleaching (% bleaching of live coral cover) and % live coral cover were measured using either a rapid visual assessment or line transects (10, 25, or 30 m depending on the organization), and transects were quantified using non-overlapping photoquadrats analyzed through CoralNet, or a line-intercept method. Some islands were monitored using ordinal bins (bleaching levels 1-5), but we elected to use only continuous (% bleaching) data to achieve a more detailed metric, which limited our
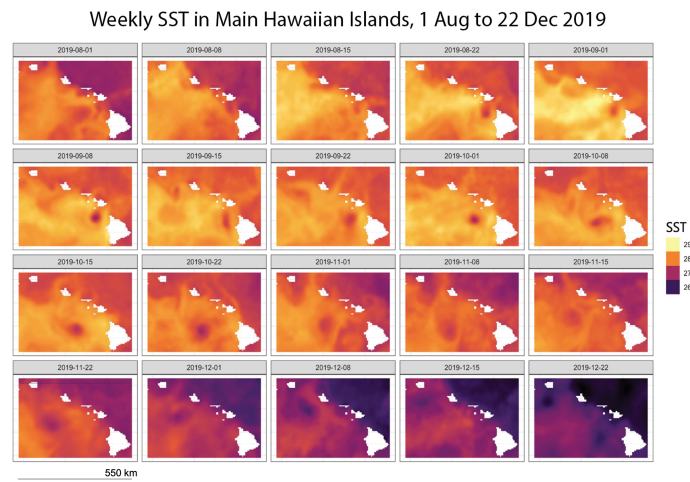
FIGURE 1

SST (°C), Main Hawaiian Islands, 01 August 2019 – 22 December 2019 aggregated from NOAA Coral Reef Watch (2019).

analysis to five islands: Hawai'i, Maui, O'ahu, Lāna'i, and Moloka'i (Figure 2A). Each survey represents a single visit to a distinct location ("site"); some locations were spaced closer together than others (see discussion of spatial autocorrelation below). While surveys included some taxon-level data, these data were not available for all locations, and we therefore did not analyze bleaching by taxon. We also decided not to analyze taxa because when several different survey techniques are used, as in this dataset, species records can vary widely between survey techniques, while % coral cover is more comparable between survey methods (Jokiel

et al., 2015). Depth was recorded for all sites but was missing for 10 observations; in these cases, we imputed depth from aircraft-based bathymetry from the Global Airborne Observatory (Asner et al., 2020a).

Turbidity

We extracted turbidity values from each site using a recently developed Shallow Water Turbidity (SWaT) method, which is
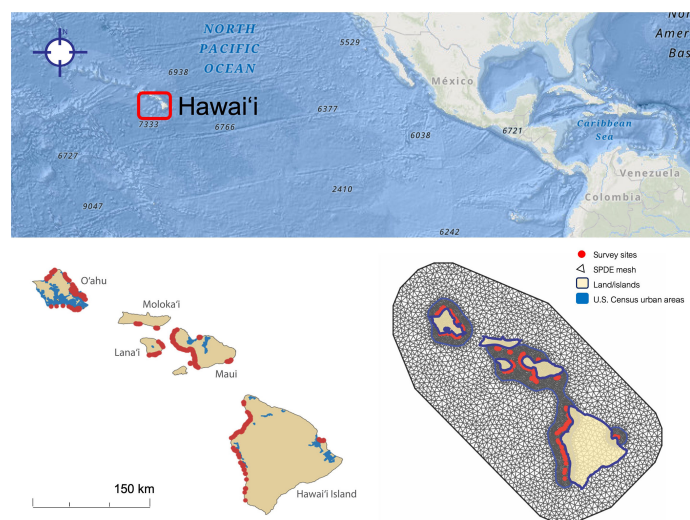

FIGURE 2

Coral bleaching site distribution (n = 1024) in five Main Hawaiian Islands. (Left) Observation sites for coral bleaching surveys (red) shown alongside urban areas (blue). (Right) Spatial mesh for modeling site spatial structure and spatial autocorrelation.

designed to detect turbidity in nearshore shallow waters using the Planet Dove satellite constellation (3.7 m spatial resolution) (Li et al., 2022). SWaT accounts for bottom reflectance in total water-leaving radiance, and therefore improves upon historical remote-sensing turbidity algorithms, which do not address bottom reflectance and therefore may overestimate turbidity values in clear, shallow, nearshore waters where bottom reflectance is high (Lee et al., 2012). SWaT was previously validated against field turbidity monitoring data from the Pacific Islands Ocean Observing System and United States Geological Service, exhibiting an accuracy of R^2 = 0.83 and RMSE = 0.90 FNU (Li et al., 2022). We extracted weekly mosaics of Planet imagery for all weeks during the bleaching event (28 July 2019 to 1 December 2019) and used bathymetry processed from Sentinel-2 data (Li et al., 2021) to subtract depth-dependent bottom reflectance from water-leaving radiance. This produced water column reflectance, i.e., the in-water turbidity signal. We then used the red band of water column reflectance to derive turbidity in Formazin Nephelometric Units (FNU) based on Dogliotti et al. (2015).

We found the maximum turbidity value within a buffer of 100 m of each survey site, which was the lowest buffer that both maximized data availability while remaining appropriate to the scale of particle mixing. We used turbidity maxima because sediment runoff often occurs in sporadic events and, therefore, turbidity regimes are well-characterized by peaks (De Carlo et al., 2007). In addition, because the SWaT algorithm subtracts bottom effects it can over-correct for bottom reflectance (underestimate turbidity) in extremely shallow areas directly abutting the coast, and therefore, nearshore surveys were more accurately represented by maxima. A visual inspection showed limited evidence of artificial outliers in imagery (discrete, extreme turbidity values) near survey points, and we found high (> 0.70) Pearson's correlation between turbidity calculated from maximum and mean values, so determined that using maxima was appropriate. All analysis was conducted using Python and the gdal library on Linux command line.

To attribute turbidity to urban sources, we created a binary variable for urban coastline using a dataset of 'urbanized areas and urban clusters' from the U.S. Census Bureau (2015) TIGER database. Survey points were snapped to the nearest coastline and considered urban if listed as 'urban' by the Census; each survey point was then manually checked against true-color satellite imagery to ensure that classification based on 2015 Census data was still accurate.

Environmental covariates

We controlled for additional bleaching drivers determined from prior literature: thermal stress, sea-surface irradiance (hereafter "irradiance"), wave power, total effluent, nitrogen runoff, depth, and distance from shore. We also examined % live coral cover as a possible confounding variable, given that high coral cover may indicate low prior bleaching and, perhaps, low vulnerability.

We derived thermal stress as both 1) SSTa and 2) Degree-Heating Weeks (DHW) from NOAA Coral Reef Watch Operational Daily Near-Real-Time Global 5-km Satellite Coral Bleaching Monitoring data (2019), obtained via ERDDAP (Simons, 2020). Since coral survey dates were inconsistent, ranging from 20 August 2019 to 7 December 2019, we extracted daily thermal data between a start date of 1 August 2019 (1 week before the Main Hawaiian Islands mean SST surpassed the regional bleaching threshold of 28.5° C) and each unique survey date. SSTa was measured as the mean daily SSTa for that period, and DHW as cumulative DHW at the survey date. SSTa and DHW were linearly related, so we selected only SSTa for analysis. We measured irradiance as the maximum Photosynthetically Available Radiation (PAR, mol m^{-2} day^{-1}) at each site during the bleaching event, derived from the MODIS Aqua satellite (NASA, 2019), which has a maximum spatial resolution of 4 km. As with temperature, we accounted for variable survey dates by fetching data between 1 August 2019 and each individual survey date. We then calculated PAR as the maximum pixel value at each point from eight-day PAR composites.

'Wave power' (kW m^{-2}) was the long-term mean of wave power (2000-2013) at each site, obtained from Kappel et al. (2017a). In this dataset, long-term means were based on hourly wave data from a SWAN (Simulating WAves Nearshore) model, which were converted to maximum daily wave power, then averaged by month from 2000-2013. While these data precede 2019, they represent the best available data for our study region and serve as a relative index of wave exposure between sites. 'Total effluent' (gal km^{-2} d^{-1}) was likewise derived from Kappel et al. (2017b), based on effluent flux from Onsite Sewage Disposal Systems (OSDS). In this dataset, OSDS flux was attributed to Tax Map Key (TMK) parcels (Whittier and El-Kadi, 2014), which were aggregated into 500-m pixels and added as total flux within a 1.5-km radius of each cell. 'Nitrogen runoff' (gal km^{-2} d^{-1}) was obtained from the same dataset.

Finally, we found 'distance from shore' as the orthogonal distance between each point and the nearest landmass. All geospatial processing was conducted using the *sf* package in R (Pebesma, 2018) and visualized in QGIS. Final independent variables for analysis were turbidity, urban area (binary), SSTa, distance from shore, depth, total effluent, nitrogen runoff, live coral cover, wave power, and irradiance (Table 1). We also tested interactions between all variables and SSTa, and the three-way interaction of turbidity, urban area, and SSTa given our interest in the source (urban v. non-urban) of turbidity.

Data analysis

We used a Bayesian hierarchical spatial model to estimate the effect of turbidity and other environmental variables on coral

TABLE 1 Mean, standard deviation, and range of unstandardized variables per island.

Island	Number of sites	Survey dates*	Turbidity (FNU)	SSTa (deg C)	Live coral cover (% benthic area)	Distance from shore (km)	Irradiance (mol m^{-2} day^{-1})	Wave power (kW m^{-2})	Nitrogen runoff(gal km^{-2} d^{-1})	Total effluent (gal km^{-2} d^{-1})	Urban (binary)	Bleaching occurence (binary)	Bleaching severity (% corals bleached)
Oʻahu	325	23/09/ 2019 – 20/10/ 2019	7.64 ± 4.08 0.10 – 17.45	0.88 ± 0.05 0.66 – 0.95	43 ± 31 1 - 95	1.16 ± 0.71 0.02 – 4.27	53.96 ± 1.72 52.08 – 58.91	4.29 ± 7.18 0 – 29.08	786 ± 1352 0 - 10492	4559 ± 8146 0 - 58532	305 Urban 18 non-Urban	280 sites Yes (1) 45 sites No (0)	0.22 ± 0.24 0 – 1.0
Hawaiʻi	276	20/08/ 2019 – 07/12/ 2019	6.33 ± 2.15 1.65 – 14.74	1.19 ± 0.17 0.65 – 1.37	36 ± 17 4 – 89	0.16 ± 0.15 0.02 – 0.89	53.89 ± 3.43 47.61 – 58.50	4.83 ± 2.91 1.15 – 14.48	1267 ± 1922 0 – 7310	7966 ± 11009 0 – 40758	73 Urban 203 non-Urban	149 sites Yes (1) 127 sites No (0)	0.08 ± 0.14 0 – 0.80
Lānaʻi	67	13/11/ 2019 – 15/11/ 2019	8.46 ± 2.81 0.13 – 19.55	1.22 ± 0.03 1.15 – 1.24	37 ± 22 2 - 95	0.21 ± 0.22 0.09 – 0.76	57.53 ± 0.73 55.94 – 58.32	3.96 ± 0.86 2.08 – 4.92	0.33 ± 1.52 0 – 7.32	0.33 ± 1.52 0 – 7.32	0 Urban 67 non-Urban	66 sites Yes (1) 1 site No (0)	0.16 ± 0.14 0 – 0.60
Maui	327	03/09/ 2019 – 13/11/ 2019	6.14 ± 2.73 1.50 – 21.33	1.19 ± 0.12 0.92 – 1.39	39 ± 25 1 – 95	0.23 ± 0.26 0 – 1.50	54.44 ± 2.64 50.11 – 58.49	3.52 ± 4.55 0.53 – 26.16	744 ± 1329 0 – 6344	3899 ± 6176 0 - 30529	121 Urban 206 non-Urban	314 sites Yes (1) 13 sites No (0)	0.28 ± 0.20 0 – 0.95
Molokaʻi	29	11/10/ 2019. – 12/10/ 2019	8.55 ± 3.66 0.67 – 15.60	1.04 ± 0.11 0.93 – 1.14	41 ± 19 15 – 80	1.51 ± 0.29 0.91 – 1.9	57.19 ± 0.67 56.48 – 58.17	4.61 ± 5.10 0.81 – 16.04	53 ± 103 0 – 296	301 ± 575 0 – 1627	0 Urban 29 non-Urban	29 sites Yes (1) 0 sites No (0)	0.21 ± 0.18 0.02 – 0.70

Categorical variables (Urban Area and Bleaching Occurrence) are listed by category.
*For each survey/site, turbidity and other covariate data were extracted only for dates between the onset of the bleaching event and survey date to prevent differences in survey date from biasing results.

bleaching. Given that our dataset contained a high number of zeros (18% of data showed no bleaching), we used a Zero-Altered approach (Zuur and Ieno, 2016) where bleaching was modeled first as a binary outcome of 'bleaching occurrence' (whether bleaching was present/absent in the survey), and data was then subset to only nonzero bleaching surveys to assess 'bleaching severity' (% bleaching of live coral cover). A Bernoulli distribution was used to fit bleaching occurrence and a beta distribution for bleaching severity, as these distributions are best suited to, respectively, presence-absence and proportional data (Zuur and Ieno, 2016). Bleaching was modeled using logit link functions as:

$$Y_i^{occ} \sim bernoulli(\pi_i)$$

$$E(Y_i^{occ}) = \pi_i \quad and \quad \sigma^2(Y_i^{occ}) = \pi_i \times (1 - \pi_i)$$

$$logit(\pi_i) = \alpha + X_i\beta + W_i$$

$$Y_i^{sev} \sim beta(\mu_i, \phi)$$

$$E(Y_i^{sev}) = \mu_i \quad and \quad \sigma^2(Y_i^{sev}) = \frac{\mu_i \times (1 - \mu_i)}{(\phi + 1)}$$

$$logit(\mu_i) = \alpha + X_i\beta + W_i$$

where Y_i^{occ} and Y_i^{sev} are bleaching occurrence and severity, E denotes fitted bleaching values, X_i is a covariate matrix of independent variables, β is a vector of regression parameters with α intercepts, μ is the mean of the beta component, π is the probability of bleaching absence vs. presence, ϕ summarizes shape parameters for the beta distribution, and W_i represents the models' spatial structure, described below.

We standardized all continuous independent variables by subtracting the mean from each observation and dividing by the standard deviation. Beta distributions only take proportional data < 1, so we converted our response variable where $Y_i = 1$ to negligibly lower values using $Y_i = (Y_i * (N-1) + 0.5)/N$, following Zuur and Ieno (2016). We assessed all variables for collinearity using Pearson's correlation index; a correlation higher than 0.70 existed between 'nitrogen' and 'total effluent' variables (ρ = 0.98, P < 0.001) so we retained only 'total effluent' for analysis (Figure

S1). We also used Point Biserial Correlation to test for correlation between categorical and continuous independent variables and confirmed that all p < 0.70. Preliminary plots of independent variables (Figure S2) indicated high positive skewness in distance from shore, depth, and wave power. Distance from shore was log-transformed, which is advised when distributions display extreme positive skewness, and wave power and depth (milder skew) were square-root-transformed. We also removed two outliers in total effluent, which represented exceptionally high values (Figure S2). Outlier removal and variable transformations had no impact on model fit > 2 DIC but improved homoskedasticity in residual-covariate plots (Figure S3).

A variogram of Pearson's residuals in initial models indicated that spatial autocorrelation existed in our dataset. We therefore modeled a spatial random effect using Stochastic Partial Differential Equations (SPDE) based on a Matern variance-covariance matrix (Lindgren and Rue, 2015; Zuur et al., 2017). To drive SPDE, we created a mesh (Figure 2B) with a nonconvex hull (convex = -0.05, concave = 0.05), which is best suited to well-separated islands, and specified maximum node distance between 1 and 10 km. We used a histogram of between-plot distances to determine range and sigma priors of, respectively, 5 km and 1 km, at 0.05 probability. We also conducted a sensitivity analysis of node distances, ranges, and sigmas, and found that variable influence was not substantially changed by priors.

To account for slight differences in survey method by organization, we included 'organization name' (identity of the organization collecting data) as a random factor in our analysis. Random effects are appropriate when correlation is expected between observations in the same group (organization), but when the relationship between independent and dependent variables is still expected to carry across all group levels (Harrison et al., 2018). Since we did not expect 'organization' to change the environment-bleaching relationship, but produce variable intercepts, a random factor was appropriate. We also included island as a fixed effect, given that islands represent different oceanographic, geomorphological, and human development regimes on reefs.

Final variables in the model were determined through backward stepwise selection, where we removed variables that did not increase model fit by 2 DIC, i.e., when only influential variables remained (Table S1-S2). We tested for homogeneity of variance by comparing residuals to all covariates, and to fitted values (Figure S3A–H). We also tested for normality of residuals (Figure S3I), and compared fitted to observed values, visually determining that the relationship was linear but not overfitted. Following Donovan et al., 2020; 2021), we considered variables influential if their 80% credible interval did not cross zero, but also assessed the 95% credible interval to identify highly influential variables (note: frequentist p-values do not apply in Bayesian statistics, but we will use the term "significant" to refer

to these influential variables, for the sake of interpretability). We used penalized complexity priors for random effects following Fuglstad et al. (2019); default vague Gaussian priors for fixed effects (mean = 0, precision = 0.001), and log-gamma priors for hyperparameters (mean = 1, precision = 0.1). All analysis was conducted using the R-INLA (Rue et al., 2009).

Results

Bleaching levels varied widely between surveys, with 18% of surveys (184 of 1024) showing no bleaching, and 25% of sites showing between 30-100% bleaching. Mean SSTa experienced by corals before survey date ranged between 0.6 and 1.4° C (Table 1). Turbidity values were evenly distributed across rural and urban areas, ranging from 0.1 FNU to 21.3 FNU (Figure 3). In addition, turbidity was not correlated with distance from shore (ρ = 0.23, P < 0.001), likely because 1) most surveys occurred within a short distance from shore (50th percentile of surveys < 200 m from shore) where strong sediment advection/ mixing is possible, 2) resuspension of bottom sediments may be variable nearshore (Jokiel et al., 2014), and/or 3) our turbidity metric was derived from a 100-meter buffer, so points 200 m apart may have had similar turbidity values. Survey regions with the highest turbidity included Honolulu and Kāne'ohe Bay, South Moloka'i, and Maui from Olowalu to Lāhainā and Kahului (Figure 3), while the region with the lowest turbidity was West Hawai'i. However, turbidity varied over fine (< 500 m) scales and was generally highest near harbors, airports, and refineries; wastewater outfalls; erosive roadsides; and steep hillsides.

The model of best fit for bleaching occurrence included SSTa, live coral cover, turbidity, urban area, distance from shore, and the interactions between SSTa-live coral cover, SSTa-urban area, SSTa-turbidity, and SSTa-urban area-turbidity (three-way interaction). For bleaching severity, the model of best fit included SSTa, turbidity, urban area, distance from shore, depth, wave power, live coral cover, and the interactions between SSTa-wave power, SSTa-urban area, SSTa-turbidity, and SSTa-urban area-turbidity (three-way interaction). All final models also included island.

Turbidity

Turbidity was a negative driver of bleaching severity (80% credible interval -0.195 < β < -0.049), and thus, turbidity decreased percent bleaching in live coral cover (Figure 4B). In contrast, turbidity did not affect bleaching occurrence (binary variable of bleaching presence/absence) (Figure 4A). The interaction between turbidity and heat stress (SSTa) was positive for both bleaching occurrence (0.098 < β < 1.121) and severity (0.139 < β < 0.373). Thus, thermal stress suppressed
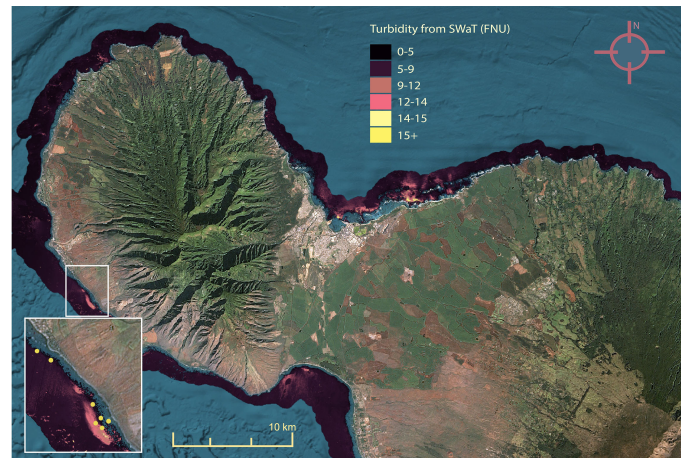
FIGURE 3
Maximum weekly turbidity (FNU) measured by Planet Dove satellites for bleaching period (28 July 2019 to 1 December 2019), magnified to Maui for detail. Inset: turbidity plume near Olowalu, HI overlaid with survey locations (yellow).

the protective effect of turbidity on bleaching severity, i.e., turbidity had a weaker effect at higher temperatures (Figure 5). In urban areas, turbidity had a largely flat effect on bleaching severity, though in non-urban areas, the relationship between turbidity and bleaching severity reversed to weakly positive (interactive effect of urban turbidity $-0.480 < \beta < -0.143$). Urban turbidity also had a negative effect on bleaching occurrence ($-1.137 < \beta < 0.462$), but this effect was not significant (Figure 4A). Urban areas, when treated in isolation without interaction, had a highly positive effect on bleaching occurrence ($0.499 < \beta < 1.894$) and no effect on bleaching severity. Therefore, the urban environment alone did

not create a protective effect on corals during the bleaching event, but the presence of urban turbidity may have indicated higher coral resistance or resilience to high temperatures (note: covariates were standardized; see Table S3 for β relative to standard deviations).

Other environmental drivers

SSTa had a positive effect on bleaching occurrence and severity, though this effect was highly significant ($0.886 < \beta < 1.848$) for occurrence only. Therefore, SSTa was a major driver
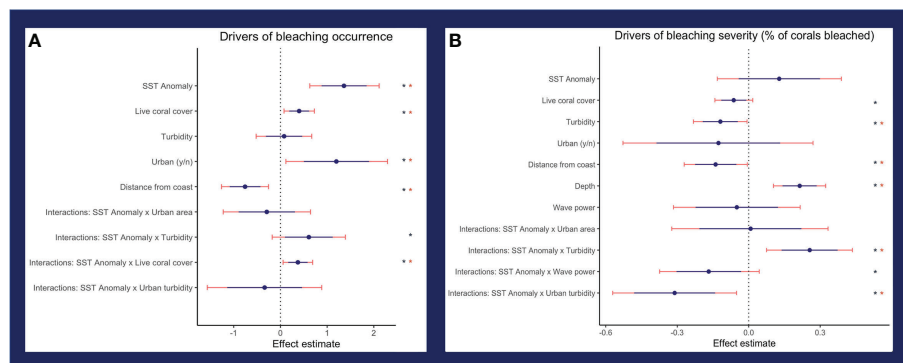

FIGURE 4
Effect of independent variables on **(A)** bleaching occurrence (binary variable for whether bleaching is present or absent) and **(B)** bleaching severity (% bleaching cover where bleaching is nonzero). Thin, pink lines show the 95% credible interval, and thick, blue lines show the 80% credible interval. One asterisk indicates significant variables (80% interval does not cross zero) and two asterisks indicate highly significant variables (95% interval does not cross zero).
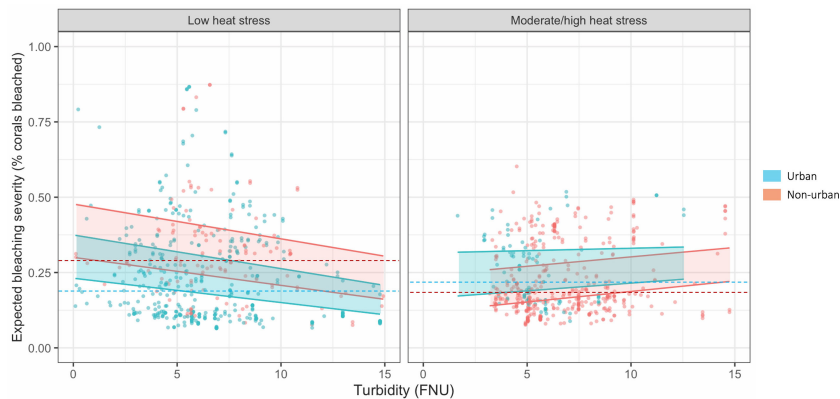
FIGURE 5
Change in bleaching severity with increasing turbidity (unstandardized) under low and high heat stress. Heat stress is divided as low <= 1.15° C SSTa and high >1.15° C SSTa, based on the 50th percentile of SSTa data. Points represent each observation in the dataset with turbidity mapped against the mean posterior estimate of bleaching severity. Bands represent fitted 80% credible interval posterior estimates for (blue) urban sites, i.e., U.S. Census-listed urban coastline, and (red) non-urban sites. Dotted lines represent median observed bleaching severity for each category. Note: In low heat stress areas, there are n = 118 non-urban and n = 408 urban sites; in moderate/high heat stress areas, there are n = 405 non-urban and n = 91 urban sites; urban areas and heat stress are not correlated > p = 0.70 (see Supplementary Material).

of whether corals bleached, but not specific levels of bleaching. In contrast, bleaching severity showed a significant dependence on the interactions between temperature and other environmental covariates such as turbidity, urban turbidity, and wave power (Figure 6; Figure S4). The interaction between wave power and SSTa had a negative effect on bleaching severity (-0.282 < β < -0.016) and therefore wave action reduced bleaching levels under increasing thermal stress.

Beyond temperature, variables associated with bleaching occurrence were % live coral cover (0.189 < β < 0.613) and distance from shore (-1.087 < β < -0.430). Areas with higher live coral cover showed a higher propensity to bleach, though this effect was weak. Corals located further from the coast were more likely to show low to no bleaching. In contrast, % live coral cover had a weakly negative relationship with bleaching severity (-0.113 < β - 0.009), as increasing live coral cover was correlated with a slight decrease in bleaching severity. Bleaching severity was higher in deeper reefs (0.145 < β < 0.286). Sea-surface irradiance was not a significant variable for either bleaching occurrence or severity.

Including island as a fixed effect dramatically reduced model DIC values, and therefore island had a strong influence on bleaching occurrence and severity. With the Big Island as a reference value, all islands showed higher bleaching occurrence and severity, although Oʻahu showed the strongest, positive effect, and Lānaʻi the weakest effect on both bleaching metrics (Figure 6). In addition, including organization name (identifier for the organization conducting surveys, which was a proxy for survey method) as a random effect substantially reduced model DIC values (-40 DIC) and thus increased model fit (Table S1–2).

Discussion

Turbidity

Turbid coral bleaching refugia have been documented worldwide, but in contrast, so have heavily damaged reefs under severe sedimentation, toxin exposure, effluent, dredging, and other turbid-area stressors (Brodie et al., 2012; Cacciapaglia and van Woesik, 2016; Carlson et al., 2019; Sully and van Woesik, 2020). By coupling high-resolution remote sensing with *in-situ* field observation, we demonstrate that turbidity may provide protection from bleaching severity but increasing temperature stress may weaken or reverse this effect, particularly in rural areas. Across the Main Hawaiian Islands, turbidity ameliorated bleaching severity overall, but thermal stress counteracted this effect, as indicated by a positive turbidity-SSTa interaction. In rural areas in particular, turbidity failed to improve coral bleaching under increased SSTa, while in urban environments, turbidity still mildly suppressed bleaching despite climbing temperatures (Figure 5). This pattern persisted when bleaching was measured as bleaching occurrence (presence/absence): turbidity decreased bleaching occurrence, though this relationship weakened as temperatures rose, especially in rural areas. Unlike for bleaching severity, these effects were not significant (80% credible interval crossed 0), likely because bleaching occurrence was overdetermined by SSTa, which was by far its most significant driver.

These findings suggest that temperature can override the protective benefits of turbidity, but that marginal reefs (chronically silty, urban areas) may have unique features that
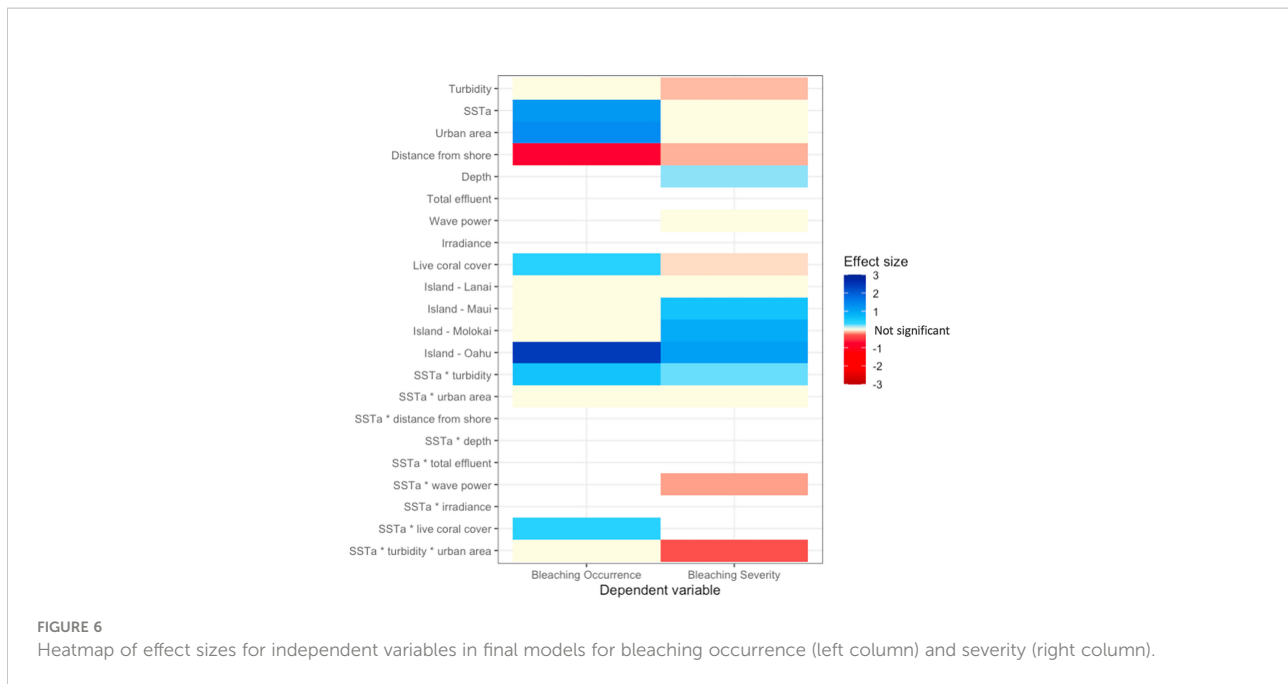
confer resilience. One possible reason for this pattern is that urban, turbid areas in Hawai'i may contain stress-tolerant corals. Urban hubs in Hawai'i have experienced prolonged disturbance, where surviving corals may have been selected over decades of intensive human contact. Stress-tolerant communities are common in urban, turbid areas, and have been observed in Singapore, Brazil, and Australia (Mora, 2008; Guest et al., 2016a; Heery et al., 2018; Loiola et al., 2019). In these regions, weedy or stress-tolerant communities have survived and/or adapted to urban trends like early grazer removal, heavy metal deposition, macroalgal proliferation, artificial habitat from urban structures, and genetic isolation (or, conversely, novel corridors) along the built coastal form (Goodkin et al., 2011; Darling et al., 2012; Heery et al., 2018). Rural areas, in contrast, represent the new development margin in Hawai'i, where earthmoving is recent and increasing. In these developing but not yet "urban" areas, coral community shifts may not have taken full course and stress-tolerant species may be uncommon or absent. Therefore, the combination of turbidity and heatwaves in rural areas may be particularly damaging. This aligns with findings by Asner et al. (2022), which linked coral mortality during Hawai'i's 2019 bleaching event to new development (conversion of "natural landscape to human-built environments" over five recent years).

Coral taxa associated with urban landscapes in Hawai'i also may have experienced more sustained pressure that begets trophic plasticity over time. Heterotrophy has been noted in turbid reefs worldwide (e.g., De'ath and Fabricius, 2010; Morgan et al., 2016), conferring resistance to bleaching through higher photosynthate translocation during heatwaves (Tremblay et al., 2016) and carbon subsidies when symbionts are lost (Grottoli

et al., 2006). However, heterotrophic taxa have been recorded in remote and urban areas alike (Zweifler et al., 2021), and further research is required to delineate the trait space of corals surviving in urban versus rural, sedimented habitats, as well as linkages between these traits and repeat bleaching susceptibility. Importantly, our results show that living in an urban environment, absent turbidity, does not confer bleaching resilience, suggesting that bleaching tolerance is limited to taxa thriving in murky segments of the urban landscape.

Previous research shows there are considerable coarse- and fine-scale morphological differences between species and phenotypes that impact coral response to sediment (Jones et al., 2016). For example, branching morphologies have been linked to higher sediment tolerance due to high surface inclination (Jones et al., 2019) but lower bleaching tolerance (Darling et al., 2012). Sediment clearing mechanisms are diverse and complex, as are morphologies designed to maximize photosynthesis (Stafford-Smith and Ormond, 1992; Guest et al., 2016b). Traits of corals surviving under low light, high sediment, and high temperature conditions along gradients of remote, urban, and developing coastlines is a critical area of research. A large portion of sites considered in our analysis did not record taxonomic data, and therefore, we were unable to evaluate taxonomic explanations for our results. Future studies should use innovative methods like rapid Structure-from-Motion photogrammetry to capture geospatial patterns in morphology over large areas, and over time (Fukunaga et al., 2020).

Another possible reason for urban refugia is that urban and rural sources of turbidity differ. The types of dissolved and particulate matter associated with urban areas may be,

counterintuitively, less harmful to corals than rural runoff at high temperatures. Urban turbidity is often associated with point-sources of pollution like wastewater treatment plants and stormwater outfalls (Carlson et al., 2019), whereas rural areas are linked to more diffuse, nonpoint sources of pollution like unpaved roads (Ramos-Scharron and MacDonald, 2005), agricultural and golf course runoff (Delevaux et al., 2018), erosion from scalded hillsides (Bartley et al., 2014), soil disturbed by feral ungulates (Tribble et al., 2016), and new construction areas, i.e., future urban sprawl (Maragos, 1993). Mills and Sebens (1997) showed that corals reject "clean" sediments. "Natural', terrigenous sources of turbidity may be most damaging to corals in Hawai'i, where lateritic, volcanic soils have small grain sizes (Storlazzi et al., 2015) that are energetically expensive for coral polyps to clear, reducing energy stores that are severely needed during thermal stress (Erftemeijer et al., 2012); however, these particles also take longer to settle out of suspension (Bartley et al., 2014). While soil runoff and fine siltation certainly occurs in urban areas, it might represent a more dominant size fraction in steep, erosive watersheds with few retaining structures, and where new construction is accelerating. Future research in Hawai'i should investigate sediment constituents and settling rates alongside bleaching severity to determine which sedimentation profiles are most associated with coral bleaching, mortality, and resilience.

Point sources of pollution, which concentrate in urban areas, are better regulated than nonpoint sources in the United States, the country of our study region (Humenik et al., 1987). Several case studies demonstrate the benefits of legally mandated, infrastructural upgrades on reef health in turbid urban waters like wastewater outfalls zones in Hawai'i. For example, after a municipal sewage system in "Māmala" Bay, Hawai'i received treatment upgrades in 1977, reefs in the bay showed no significant evidence of sewage impact (Grigg, 1995). Likewise, sewage upgrades in 1978 in Kāne'ohe Bay resulted in a doubling of coral cover from 12% in 1971 to 26% in 1983 (Hunter and Evans, 1995). If rural areas are more difficult to regulate, or last in line for infrastructural improvements, they may drive a higher toxic load on reefs from facilities like leaking cesspools/underground storage tanks (Yoshioka et al., 2016; Abaya et al., 2018). Finally, our results align with a recent meta-analysis on bleaching susceptibility in human-dominated and isolated reefs (e.g., atolls), which provide limited evidence for "remote refugia" but indicate some resilience in human-dominated habitats (Baumann et al., 2022). In particular, our results suggest that regions that are not yet developed but show symptoms of new development (non-urban turbidity) may be particularly susceptible to coral bleaching.

Our results do not imply that urban turbidity creates a 'safe haven' for coral reefs. We did not evaluate coral disease, diversity, fecundity, size classes, calcification rate, or other elements of coral health in our analysis, and it is possible that corals in silty, urban areas are stress-tolerant but sparse,

homogenous, or otherwise represent ecosystem phase shifts. However, our results support past case studies (e.g., Guest et al., 2016b) by indicating that urbanization can counterbalance thermal stress during bleaching events. We further add that, in rural areas, turbidity does not counteract heatwaves, and runoff from new development, agriculture, unpaved roads, and nonpoint sources of pollution may still pose a critical threat. In Hawai'i, rural areas may represent a combination of unchecked earthmoving, new dredging, and aging infrastructure, which require urgent intervention.

A recent study indicated that mortality is highest when thermal stress and dredging conditions (high suspended sediment, low light) occur together (Fisher et al., 2019). While corals bleached less under low/moderate light reduction, severe light limitation acted synergistically with thermal stress to increase mortality. We likewise find that turbidity only acts antagonistically against bleaching under certain conditions (low heat stress). More research is needed on the nuanced thresholds of light, irradiance, and heat that alter interactions between stressors for various coral species.

Our findings are inconsistent with one hypothesis of turbid refugia—that sediment shades corals from excessive sunlight (Anthony et al., 2007). Equivalent levels of rural and urban turbidity should have the same effect on coral bleaching if protection comes from light-shading alone. Instead, in our study, turbidity associated with different land uses affects bleaching differently. At low levels of SSTa, rural areas show a slightly steeper decline in bleaching severity than urban areas. Conversely, at high SSTa, an equivalent increase in turbidity provides less bleaching protection in rural areas compared to urban areas (Figure 5). However, turbidity levels may be relatively moderate in the Hawaiian Islands compared to other regions where turbid refugia have been studied. For example, Morgan et al. (2016) found that turbidity in Paluma Shoals, Australia caused 100% attenuation of Photosynthetically Active Radiation (PAR) at 4 m water depth, relative to turbid reefs in Hawai'i like Puhi Bay where we previously measured ~72% attenuation of PAR at 5 m depth in preliminary experiments. Rural turbidity may still protect corals from excessive irradiance during bleaching events in regions where turbidity levels are high (van Woesik et al., 2012; Cacciapaglia and van Woesik, 2016; Morgan et al., 2017) though, as discussed, suspended sediment and excessively low light can also induce bleaching and mortality in corals (Fisher et al., 2019).

Other environmental drivers

When estimating the impacts of SSTa alone, we found that SSTa was an extremely strong predictor of bleaching occurrence, but not severity. However, the interactions between SSTa and local environmental variables (turbidity, urban turbidity, and wave power) had a very strong effect on bleaching severity.

Specifically, under increasing SSTa, turbidity exacerbated bleaching severity, but urban turbidity and wave power reduced bleaching severity (Figure 4B). Overall, our results show that temperature, expectedly, is the most important factor determining whether corals bleach, but SSTa interactions with local environmental variables determine whether bleaching is minor or severe. Often, studies do not differentiate between bleaching occurrence and severity, and our results highlight additional insights gained through this approach. Irradiance showed no significant relationship to coral bleaching occurrence or severity, perhaps because our remotely sensed irradiance metric captured light on the ocean surface but not at depth, and corals in our analysis experienced a wide range of in-water light-scattering conditions. Indeed, since turbidity is a light-based metric, turbidity likely captured some variability in irradiance at depth. In addition, the effect of SSTa, irradiance, and other environmental variables may have been moderated by the lower resolution of those data (e.g., 5 km for SSTa, 4 km for irradiance, 500 meters for total effluent) relative to turbidity; nonetheless, these were the best data available.

Our results highlight the importance of SSTa-environment interactions, which is consistent with growing literature on the impact of local drivers on coral reef health (Graham et al., 2015; Cinner et al., 2016; Ellis et al., 2019; Donovan et al., 2021). Local variables (e.g., wave action, upwelling, internal waves, tides, mangrove refugia, and other features) alter coral exposure to thermal stress and ability to cope with and recover from bleaching (West and Salm, 2003). In two global analyses using Reef Check data, interactions between SSTa and local conditions including turbidity, wave power, and macroalgae were found to mediate bleaching severity (Sully and van Woesik, 2020; Donovan et al., 2021). In our analysis, wave power negatively influenced SSTa effects on bleaching severity, perhaps because waves increase mass transfer of oxygen radicals from coral tissues (Nakamura and van Woesik, 2001), thereby reducing host stress. Waves may also have caused ocean cooling at finer scales than the thermal signal detected by satellites. Live coral cover was linked to increased bleaching occurrence but decreased bleaching severity. One possible explanation is that high coral cover increases the probability of observing any (even minor) bleaching on a survey, but also indicates areas where corals survived prior bleaching in Hawai'i (high bleaching resilience). Overall, interactions between local environment and regional heatwaves is a critical area of ongoing research, and advances in remote sensing can enable a granular, scalable understanding of these dynamics.

Including island as a fixed effect increased model fit, and in particular, three islands (Maui, Moloka'i, and O'ahu) showed increased bleaching severity relative to Hawai'i. Moloka'i is largely undeveloped but exhibited the highest turbidity of any island (Table 1), likely because numerous surveys were located on the heavily sedimented south shore of the island where terrigenous

sediment is deposited from several drainage basins (Ogston et al., 2004; Jokiel et al., 2014). O'ahu, in contrast, is highly urbanized with variable turbidity and low coral cover proportional to substrate area (Asner et al., 2020b), though O'ahu surveys displayed a mean 43% live coral cover and surveys may therefore have focused on higher-coral areas. Maui represents a mixture of urban and rural areas experiencing sewage discharge and bottom sediment resuspension in urban centers (Laws et al., 2004) and increasing development and agriculture in remote regions (Oleson et al., 2017). Given this complex array of factors, it is difficult to interpret island-based results without additional investigation, but it is possible that site selection may have played a role in island influence (e.g., excluding the north and west sides of Moloka'i).

Finally, it should be noted that including 'organization name' as a proxy for survey method substantially increased model fit in all cases, pointing to the need to control for survey biases in coral research. Nonetheless, when using broad metrics like percent bleaching, past research has shown that coral survey techniques yield comparable results (Jokiel et al., 2015).

Implications for management and research

This study is an early step in using high-resolution satellite monitoring to characterize possible turbid refugia. We considered broad categories of turbid landscapes (urban and rural), which should be refined in the future to include a full spectrum of land-use classes such as agriculture, forestland, grassland/scrub, suburban and residential areas, and others. In addition, recent research points to the importance of temporality in turbidity regimes (persistent, fluctuating, and transitional turbidity) in dictating coral health (Zweifler et al., 2021). Planet Dove satellites, which offer a daily revisit frequency, can help characterize differences in the timing of turbidity, and identify which temporal regimes are linked to bleaching protection or harm. Importantly, the methods we highlight here may be highly useful to local managers. High-resolution satellite data can help coastal decision-makers identify specific plumes, resuspension areas, and other sources of turbidity to address runoff on a case-by-case basis. For example, where heavy plumes are linked to bleaching refugia, managers may prioritize coral protection by addressing persistent stressors like pathogens and disease, while frequently monitoring for algal overgrowth. Turbid areas associated with coral decline, on the other hand, should be prioritized for complete remediation. High-resolution satellite data can also be used to help refine existing models for predictive purposes, and scaled to local suspended sediment concentrations to monitor sediment against known coral health thresholds.

Data availability statement

The original contributions presented in the study are included in the article/Supplementary Material. Further inquiries can be directed to the corresponding author.

Author contributions

RC conceived the study, conducted the analysis, and wrote the manuscript. GA conceived and funded the study and contributed to the analysis and writing of the manuscript. All authors contributed to the article and approved the submitted version.

Acknowledgments

Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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Supplementary material

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fmars.2022.969472/full#supplementary-material

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