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Complex drivers of invasive macroalgae boom and bust in Kāne'ohe Bay, Hawai'i

Morgan Winston [a,b,*], Kimberly Fuller [c], Brian J. Neilson [c], Mary K. Donovan [a,b]

[a] School of Geographical Sciences and Urban Planning, Arizona State University, Tempe, AZ 85281, USA
[b] Center for Global Discovery and Conservation Science, Arizona State University, Hilo, HI, USA 96720
[c] State of Hawai'i Division of Aquatic Resources, Honolulu, HI 96813, USA

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ABSTRACT

Invasive macroalgae *Eucheuma* sp. and *Kappaphycus* spp. (E/K) became a dominant benthic feature in Kāne'ohe Bay throughout the past four decades - occurring on up to 74 ha of reef area and growing up to three meters thick, which prompted intensive management action. In 2013, E/K cover began decreasing at managed and unmanaged sites. This study examined the extent and timing of the E/K decline and evaluated environmental and ecological drivers beyond management contributing to the decline. E/K continued to recede into 2017 and remains sparse in Kāne'ohe Bay today. Increasing over the sampling period, herbivore biomass was negatively correlated with E/K cover, and other significant, non-linear relationships emerged between E/K cover and coral cover, sea surface temperature, wind, and rainfall. This study uncovers several possible mechanisms explaining a boom and bust in E/K abundance, emphasizes the importance of herbivory, and highlights the resilience of coral reefs in Kāne'ohe Bay.

1. Introduction

Benthic algae provide critical ecological functions in healthy coral reef ecosystems. On a stable reef in a coral-dominated state, macroalgae are distributed in relatively low abundance, and serve vital roles in primary productivity and the retention and recycling of nutrients (Smith et al., 2002; Fong and Paul, 2011), and as food sources and habitat for larval fish recruits, mobile and sessile invertebrates, and larger herbivores (Forbes, 1996; Bolam and Fernandes, 2002; Wilson et al., 2010). However, uncontrolled macroalgal growth threatens the structure and function of coral reefs through direct competition and contact with corals (e.g., shading, abrasion, overgrowth, and space occupation) (River and Edmunds, 2001; Jompa and McCook, 2002; Hughes et al., 2007; Foster et al., 2008). Macroalgae can further alter the aquatic environment through the release of dissolved organic carbon (DOC) into the water, which can fuel harmful microbial activity and induce coral bleaching and mortality (Smith et al., 2006; Barott et al., 2009). The proliferation of macroalgae has become increasingly common on reefs for a myriad of reasons, stemming from a rise in climate change and human activity triggered disturbances (Cannon et al., 2023), which have also led to an upsurge in the introduction of non-native species worldwide (Schaffelke et al., 2006). Non-native and invasive algae are spread as a result of both indirect and direct actions through multiple vectors, including biofouling of vessel hulls, ballast water discharge, aquarium trade, and mariculture experimentation and production (Ruiz et al., 2000; Zemke-White and Smith, 2006; Williams and Smith, 2007).

The success of invasive macroalgae species in novel habitats is often a consequence of anthropogenic disturbances and the intrinsic biological and environmental qualities of the local ecosystem. Undisturbed coral reefs are often more resilient and resistant to invasions, while reefs under stress are more susceptible to invasion and subsequent proliferation of introduced macroalgae (Byers, 2002), which may have been selected via mariculture experimentation for fast growth and high reproductive rates, as well as vegetative propagation (Naylor et al., 2001; Ask and Azanza, 2002) – traits that enable these macroalgae to outcompete native algal species and overgrow reef-building corals. There are several potential drivers of invasive algae proliferation, including eutrophication due to land-based pollution and reduced herbivory. Increased terrestrial nutrients in reef ecosystems due to sewage effluent can drive algal growth (Stimson et al., 2001). Low herbivore biomass, often as a result of unsustainable fishing practices and habitat degradation, has also been associated with the increasing dominance of invasive macroalgae on reefs (Stimson et al., 2001; Smith et al., 2002; Stamoulis et al., 2017).

* Corresponding author at: School of Geographical Sciences and Urban Planning, Arizona State University, Tempe, AZ 85281, USA.
E-mail address: mwinsto2@asu.edu (M. Winston).

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The Hawaiian Archipelago has a long history of introduced and invasive algae species. Since the 1950s, there have been 20 different species of macroalgae introduced purposefully (for food or aquaculture) or accidentally (by hull-fouling) to Hawai'i (Smith et al., 2002; McDermid et al., 2019). This includes three Eucheumoid species of the genera *Kappaphycus* and *Euchuema* (hereafter referred to as E/K due to inconsistencies in nomenclature) that were purposefully introduced from the Philippines to Kāne'ohe Bay, Hawai'i in the 1970s for aquaculture research (Doty, 1977; Russell, 1983). This introduction resulted in a dramatic phase shift from a coral to macroalgal-dominated state throughout patch reefs in Kāne'ohe Bay. By 1996, E/K spread throughout the Bay, beyond 5 km from its initial point of introduction on Moku O Lo'e Island (Rodgers and Cox, 1999). Unchecked for more than two decades, E/K was observed on most patch and fringing reefs in both the south and central portions of the Bay and continued to expand its range, spreading to northern reefs adjacent to Kāne'ohe Bay by 1999 (Conklin and Smith, 2005). By 2001, E/K was detected on nine reef flats and its cover averaged 40 % across the sites surveyed (Smith et al., 2002).

The E/K complex was especially threatening to Kāne'ohe Bay's coral reefs due to its rapid growth and formation of dense mats, leading to the shading and smothering of live coral that often resulted in coral mortality (Woo, 2000; Chandrasekaran et al., 2008; Stimson and Conklin, 2008). E/K has also thrived due to its propagation reproductive strategy and subsequent dispersal dominated by vegetative fragments (Woo, 2000; Smith et al., 2002). Due to the threats of E/K on the coral reefs of Kāne'ohe Bay and beyond, as well as its relatively limited distribution compared to other invasives, like *Gracilaria salicornia* and *Acanthophora spicifera*, the management of this complex was deemed a priority by the State of Hawai'i. A large-scale removal project began in 2008 on multiple patch reefs across Kāne'ohe Bay, following extensive testing of control methods by local managers, community members, and researchers (Neilson et al., 2018; Conklin and Smith, 2005). Mitigation efforts at most reefs were composed of a two-phase technique, where both manual removal by divers was conducted (using an underwater vacuum system or by hand) as well as outplanting of the native herbivorous short-spined sea urchin *Tripneustes gratilla* (Neilson et al., 2018). Reducing the standing crop of E/K prior to beginning urchin biocontrol was found to decrease the number of urchins and ultimate cost required to treat a reef; therefore, the treatment of most reefs over the mitigation period began with one period of manual removal, followed by multiple outplantings of urchins per year. These management practices of E/K by the State of Hawai'i were shown to be effective approaches for controlling macroalgal proliferation and sustaining low cover on Kāne'ohe Bay's reefs (Neilson et al., 2018). However, field crews began to notice a prominent decline in E/K on both treatment and control reefs beginning in 2013 (Fig. 1), leading to the hypothesis that other drivers besides management were driving declines.

Using field observations from multiple patch reefs across Kāne'ohe Bay, the objectives of this work were twofold. First, this study aimed to document the decline in abundance of E/K from 2011. The second aim of this study was to relate the E/K change over time to potential drivers by pairing spatially extensive timeseries of E/K abundance with bay-wide and reef-scale environmental and ecological data while accounting for variation due to past management. E/K thrives under specific environmental conditions; therefore, variability in certain factors such as

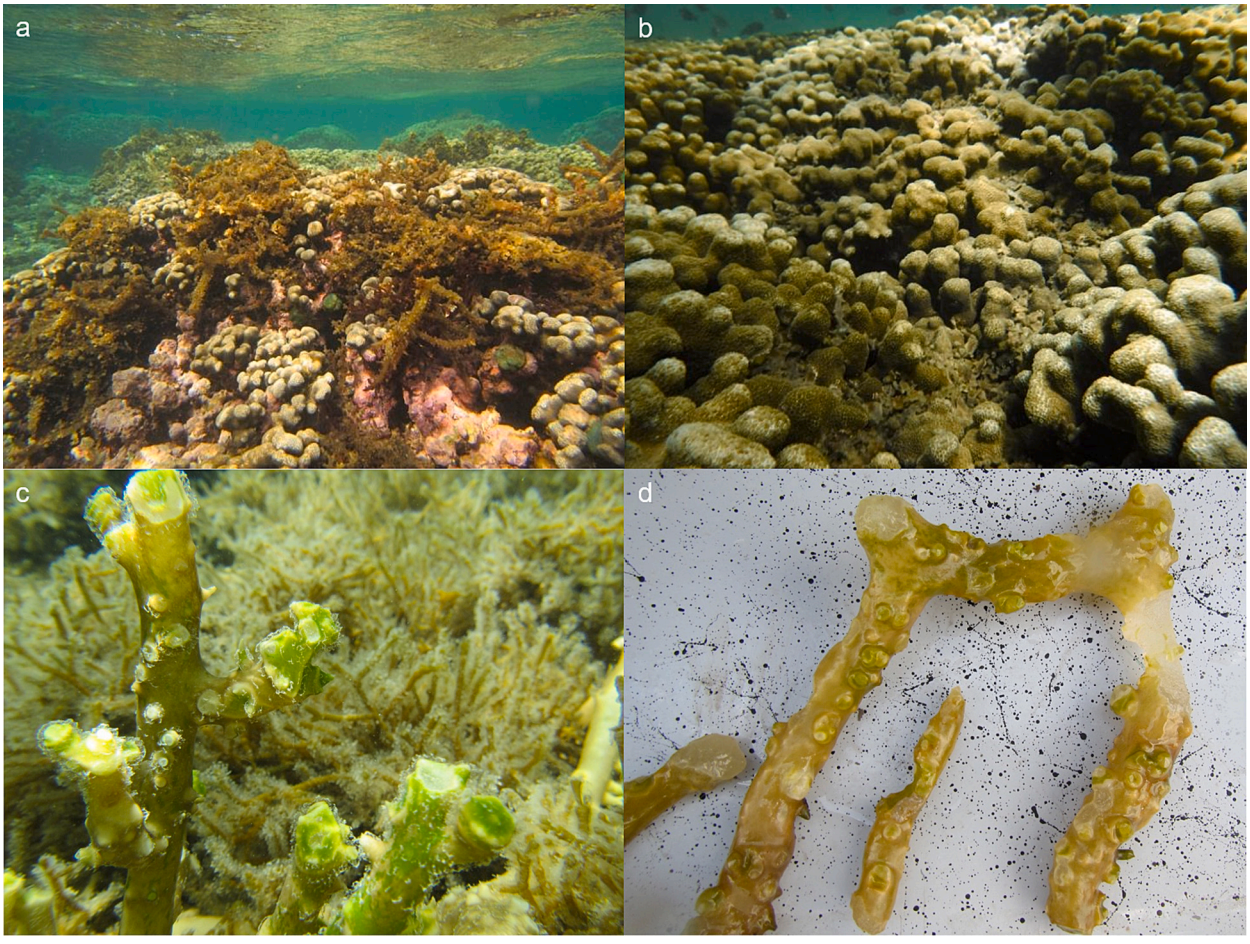

Fig. 1. Eucheumoid species of the genera Kappaphycus and Euchuema (E/K) in Kāne'ohe Bay prior to decline in cover outcompeting live coral (a), found in crevices amongst coral in November 2018 after likely being grazed down by herbivores (b), and with evidence of bite marks from herbivorous reef fish (c and d).

temperature, salinity, nutrients, water motion, and surface light may have played a role in the decline (Glenn and Doty, 1990). Based on prior patterns of invasive algae decline observed in Kāne'ohe Bay (Stimson and Conklin, 2008) and documented growth patterns of E/K, certain water temperature, freshwater, and surface light thresholds could lead to decreases in abundance, whereas increased water motion may be beneficial for the growth of E/K. In 2014 and 2015, Kāne'ohe Bay experienced consecutive heat stress events that led to widespread coral bleaching and mortality (Bahr et al., 2015, 2017). While the loss of coral cover due to post-bleaching mortality would be expected to open space for competitive macroalgae such as E/K to expand into, this theoretical advantage for E/K is confounded by the potential adverse effect of extreme temperatures on E/K itself during heat stress events. Coral populations in Kāne'ohe Bay have also exhibited remarkable resilience over time to acute and chronic disturbances (Stimson, 2018; Johannsen et al., 2022). Further, herbivory may play a role in regulating the abundance of E/K given the prominent role of herbivores in determining reef state (Green and Bellwood, 2009), particularly browsers due to their

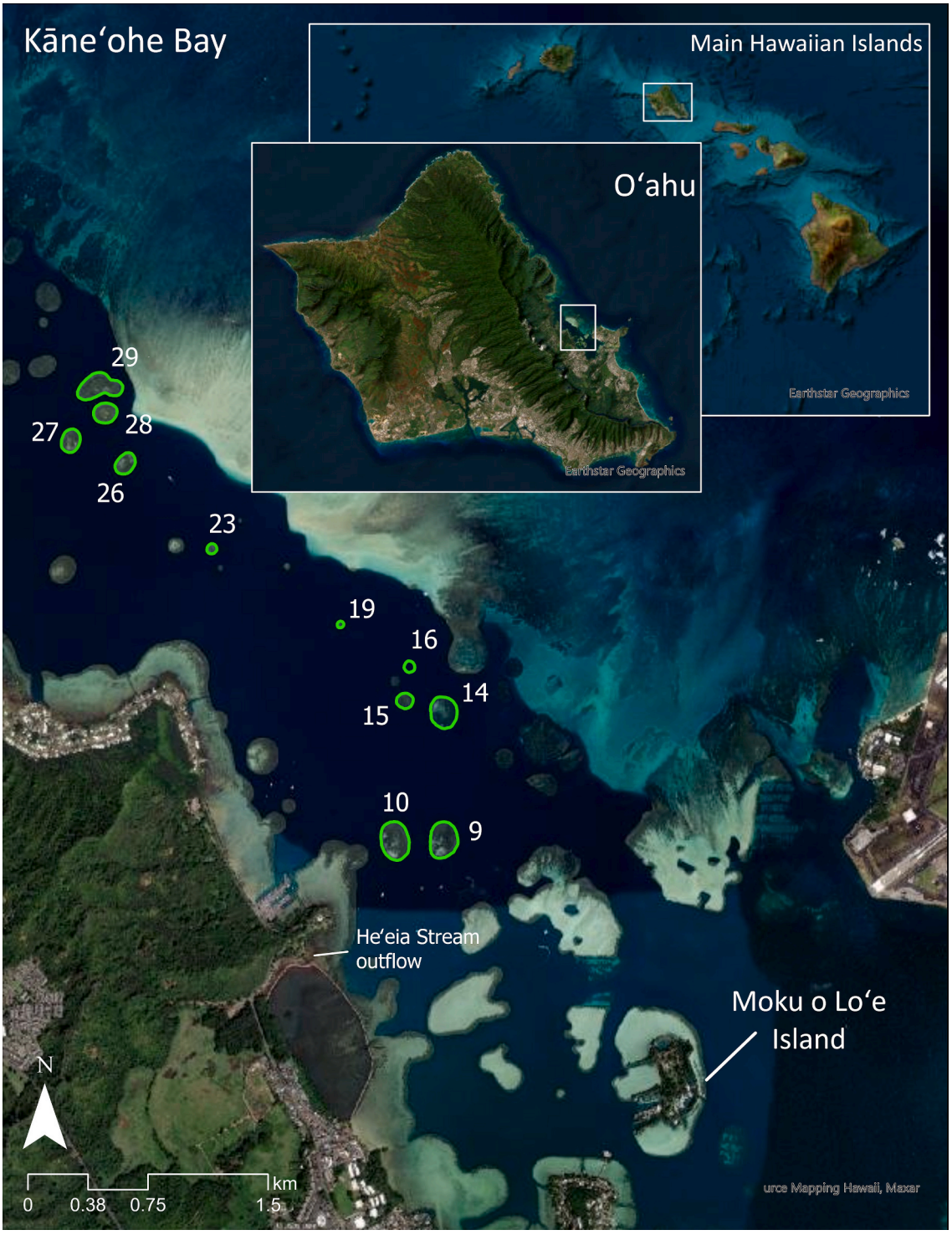

Fig. 2. Patch reef locations in Kāneʻohe Bay (O'ahu, Hawai'i) where benthic and fish surveys were performed from 2011 to 2019, and Moku o Lo'e Island, where the PacIOOS weather station is located.

documented consumption of invasive macroalgae in Kāne'ohe Bay (Stamoulis et al., 2017).

2. Materials & methods

2.1. Site description

Kāne'ohe Bay is located on the windward side of the island of O'ahu and is the largest embayment in the main Hawaiian Islands. Kāne'ohe Bay is composed of a series of over 60 small, shallow patch reefs ranging from 30 to >200 m in diameter (Fig. 2), each with a unique and established identification number. The shallower reef flat of each patch reef tends to be composed of a mixture of live and dead coral, rubble, and sand, while reef slopes are largely dominated by live coral which declines with depth to the bay bottom at ~15 m (Hunter and Evans, 1995; Neilson et al., 2018). Reefs in Kāne'ohe Bay have experienced a long history of anthropogenic influences, due to both rapid human population growth as well as poor land and water management practices that have led to historically high levels of sewage discharge and sedimentation (Bahr et al., 2015). However, reefs here have been shown to be highly resilient to local stressors, with corals demonstrating higher resistance to acidification and temperature increases than other corals around O'ahu (Jury and Toonen, 2019).

2.2. Invasive algae and coral percent cover

Benthic cover surveys have been conducted on a number of patch reefs in Kāne'ohe Bay since 2011. To determine the range and degree of the decline of invasive macroalgae E/K, we combined data from two types of surveys that covered a total of 11 patch reefs between 2011 and 2019 (Table S1).

A line-point-intercept (LPI) transect method (Hill and Wilkinson, 2004) was used to estimate the percent benthic cover of invasive macroalgae, E/K (*Eucheuma* clade E, *Kappaphycus* clade B) and live coral from November 2011 to February 2018. Cover was recorded at 0.2 m intervals along each 25 m transect (n = 126 points transect^{-1}). The number of transects per reef varied according to reef size at an average sampling effort of one transect per ca. 800 m^2 (S Fig. 1). Fixed transect locations were randomly selected within the following strata: windward and leeward prevailing wind orientation, and habitat type (aggregate reef, mixed/unconsolidated reef, and pavement/consolidated reef situated on reef flat and reef slope areas). Transect start and ends were spaced at least 10 m apart from each other in all directions, and individual transects were constrained to one strata type. Reef slope transects were oriented clockwise around a reef, with the center of the transect following the crest of the patch reef.

Photo quadrat (PQ) transects were conducted using a camera that was secured on a custom PVC quadrat frame fixed 50 cm above the benthos to capture a 40 cm × 50 cm photo frame from September 2014 to October 2019. Photos were taken every 50 cm on both sides of a 10 m transect, totaling 40 photos per transect. Twenty random stratified points per photo were assigned benthic identifications using Coral Point Count with Excel extensions (CPCe) and CoralNet (Beijbom et al., 2015) to calculate percent cover of benthic taxa. Each patch reef had twelve 10 m long fixed transects, the location of which were chosen using a stratified random sampling approach generated using ArcGIS software with four transects located on the reef slope and eight located on the reef flat.

We visually examined the trend in E/K cover over time by summarizing and plotting reef-scale percent cover per survey date over method and habitat type.

2.3. Environmental variables

Sea surface temperature (SST [°C]), wind speed (mph), photosynthetically active radiation (PAR [μmol m^{-2} s^{-}1]), and rainfall (mm) are continually monitored and were obtained from the Pacific Islands Ocean Observing System (PacIOOS) weather station located at the Hawai'i Institute of Marine Biology (HIMB) on the island of Moku o Lo'e in Kāne'ohe Bay (Fig. 2, Rodgers et al., 2005). To associate abiotic data with benthic cover data, we calculated the daily average (SST and wind speed) or sum (rainfall and PAR) of each variable. Due to calibration issues and missing data from the weather station, intermittent gaps in the environmental data occurred during 2016, 2018, and 2019. Therefore, the daily average of each value per month was calculated using historical data (not including that collected in 2016, 2018, and 2019) and used to fill in missing days of data. The mean (SST, wind speed, and PAR) or maximum (rainfall) of the variables were then calculated for the 30-day period prior to and including each benthic survey date.

Over the timespan of benthic surveys, two consecutive heat stress events occurred in 2014 and 2015 in Kāne'ohe Bay. Therefore, we also generated degree heating weeks (DHW) per survey, a common measure for the accumulation of heat stress experienced (Eakin et al., 2007). We first calculated the daily average of SST using the PacIOOS SST data. We then calculated DHW as the time spent above 28 °C (mean monthly maximum [MMM] + 1 °C for Kāne'ohe Bay; Jury and Toonen, 2019) during the most recent 12-week period prior to each survey (Liu et al., 2015).

2.4. Fish density and biomass

Fish surveys were conducted within four 25 × 5 m belt transect areas in conjunction with benthic cover surveys to identify and estimate the size of fishes at each fixed LPI and PQ site from 2011 to 2019. At fixed LPI sites, fish surveys were conducted along the same 25 m transect line. Fish surveys of PQ sites were performed by surveying an area that combined two 10 m PQ transects with a 5 m distance in between. For both LPI and PQ surveys, surveyors swam approximately 10 min transects recording the size class and species of all fishes observed within 2.5 m on each side of the transect tape. Fishes were counted according to the following size classes: 0–5 cm (A), >5–10 cm (B), >10–15 cm (C), >15–20 cm (D), and >20 cm (E). Total length was estimated to the nearest 1 cm for any fish larger than 20 cm. For all fish surveys we accounted for differences in counts of schooling parrotfish (*Chlorurus spilurus* and 'unknown parrotfish') amongst observers by adjusting large values based on previously collected data from Kāne'ohe Bay collected by experienced fish surveyors (Stamoulis et al. (2017)). We calculated the 99th percentile of school counts for size classes A, B, and C for observed *C. spilurus* and for all other species of parrotfish observed combined. Any school count in our fish dataset that exceeded this 99th percentile was replaced with the 99th percentile calculated from the Stamoulis et al. (2017) data by size class. Total length (TL) estimates were converted to weight (W, grams) per species using the allometric growth equation: $W = aTL^b$, where a and b are species-specific growth constants with Hawai'i-specific parameters where possible (Donovan et al., 2018), or from Fishbase (Froese and Pauly, 2022). Fish species were classified into herbivorous functional groups (grazers, scrapers, and browsers) following Donovan et al., 2018 (Table S2). Average fish biomass was calculated across all surveys per survey month and habitat (slope vs. flat) for each patch reef to pair with benthic data, given slight temporal differences in fish versus benthic surveys. At some reefs, benthic surveys did not have fish surveys conducted during the same month. For these reefs, fish surveys that were conducted during the closest month to the benthic survey were used only if the fish surveys were conducted within 60 days of the benthic survey. All available herbivorous reef fish data were used to visually investigate the temporal trend in herbivorous fish biomass.

2.5. Statistical analysis

All data were analyzed using R Statistical Software 3.6.3 (R Core Team, 2020). Drivers of the decline in E/K over time were examined by

constructing a single generalized additive mixed effect model (GAMM) fit by restricted maximum likelihood with a Gaussian distribution in the *mgcv* package (Wood, 2017). The response variable (E/K percent cover at the transect level) was square-root transformed to meet assumptions of normality. Ecological predictors, including herbivore biomass and percent cover of live coral, along with environmental predictors (SST, PAR, wind, and rainfall) were included as fixed effects. Prior to inclusion in the model, predictor variables were examined for collinearity (with a threshold correlation of 0.6 for inclusion) and standardized to a zero mean and unit variance to align values of different magnitudes. Smoothing terms were included for continuous predictor variables to estimate the potential for non-linear relationships, and knots were limited to four to prevent overfitting (Zuur et al., 2009). Time was included as a fixed effect represented as an integer with one equal to the starting year, and to account for temporal autocorrelation we included an autoregressive lag-1 correlation with time. Treatment was also included as a fixed effect in the model. Treatment is a reef-specific binary variable dependent on whether the date of benthic survey occurred prior to or following the first instance of manual algal removal or urchin biocontrol (Table S3). The random effects included in these models were method (LPI vs. photoquadrat), habitat (reef flat vs. slope), and reef identity. The inclusion of reef as a random effect accounts for the likelihood of spatial autocorrelation in the data and site-level variability not explained by the fixed effects. Residual plots were used to check model assumptions.

To visualize differences in herbivore functional group biomass across surveys with varying levels of E/K cover we conducted non-metric multidimensional scaling (nMDS) with the 'metaMDS' function in R, which uses up to 20 random starts to solve for an optimal solution based on standardized scaling while calculating both site and species scores (Legendre and Legendre, 2012). We also examined the relationships between E/K cover and the biomass of each herbivore functional group (browsers, grazers, and scrapers) by running a redundancy analysis (RDA) with the 'rda' function in R. Redundancy analysis is a constrained ordination method that relates linear combinations of the response variable (E/K cover) to explanatory variables (herbivore functional group biomass) (Legendre and Legendre, 2012). All metrics were summarized by taking the mean across year, month and reef. Herbivore functional group biomass metrics were log +1 transformed, and E/K cover was square root transformed. Each metric was standardized between zero and one such that all metrics were on similar scales. Permutation tests were used to test the overall significance of the model and of the constrained axes using the 'anova.cca' function in R. All multivariate methods were conducted in the *vegan* package in R (Oksanen et al., 2019).

All data and R scripts used to perform analyses and prepare figures can be accessed on GitHub (Winston et al., 2023).

3. Results

The percent cover of E/K on Kāne'ohe Bay's patch reefs exhibited a significant, non-linear decline over the survey period of November 2011 to September 2019. While not all patch reefs were surveyed across the same survey window (Table S1), the majority experienced a robust decline in E/K cover from 2013 to 2015, after which time E/K stabilized at low cover (Fig. 3). With the exception of Reefs 26 and 27, where invasive algae mitigation efforts began respectively in January 2011 and March 2012, E/K treatment did not begin in force for other reefs until 2014 due to funding limitations, when natural algal decline was already underway. From 2015 onward, E/K remained low, until cover began to slightly increase in 2018 at some reefs (Fig. S1). However, cover remained close to 0 % at the majority of surveyed transects. Over the entire survey period, Reef 16 had the highest cover of E/K amongst reefs surveyed, with a maximum mean of 35.2 % observed across all surveys completed in March 2013. E/K still declined precipitously at Reef 16 by November 2015, when <1 % mean cover was recorded.

The GAMM of multiple drivers over time [herbivore biomass, live coral cover, SST, wind speed, rainfall, PAR, and DHW] explained 55 % of overall variation in E/K cover (Table S3). Herbivore biomass emerged as a significant driver of E/K decline across patch reefs in Kāne'ohe Bay ($p < 0.001$, Fig. 4). Herbivore biomass rose over time (Fig. 5), with the greatest rate of increase beginning in early 2014. From 2011 to 2013, mean herbivore biomass was generally low, and declined overall across reefs from 3.53 to 1.08 g m^{-2}. Herbivore biomass then began to sharply

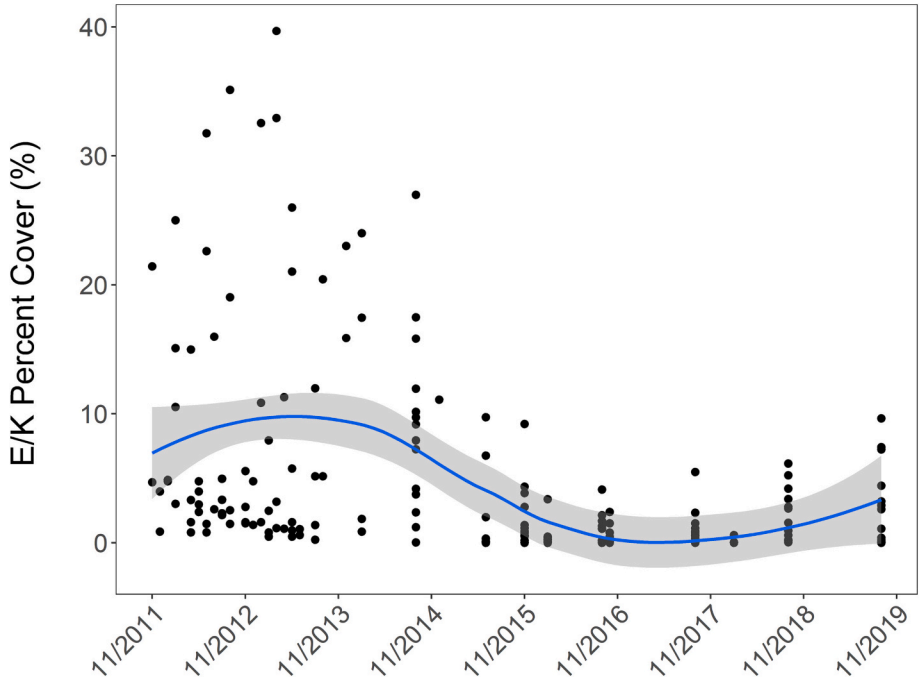

Fig. 3. Temporal trend in E/K percent cover (%) from 2011 to 2019 fit using a loess smoother. Points represent mean cover summarized per method (LPI vs. PQ) and habitat (flat vs. slope) at the reef scale.

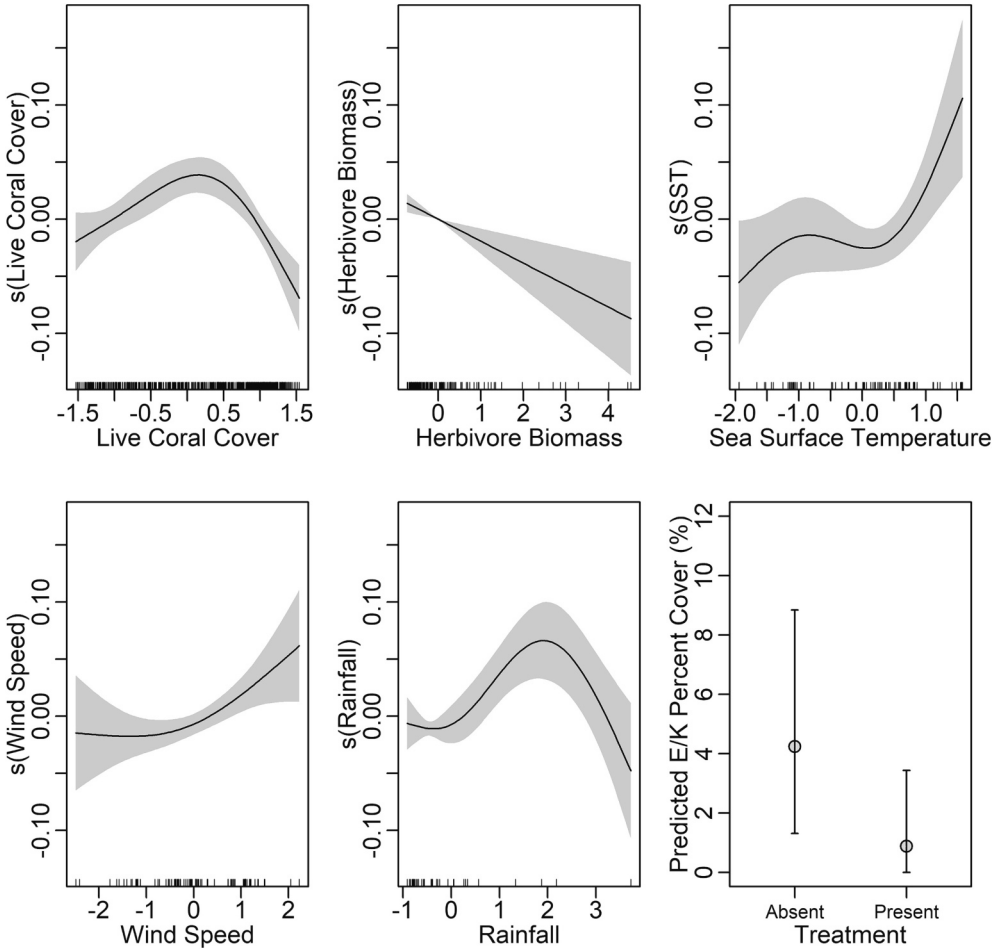

Fig. 4. Generalized additive mixed model (GAMM) model results showing the partial effects of scaled predictors that were significantly associated with E/K percent cover (live coral cover, herbivore biomass, sea surface temperature, wind speed, and rainfall), where shaded areas represent 95 % confidence intervals for the predictor effect. Model predictions are shown for management treatment with 95 % confidence intervals.

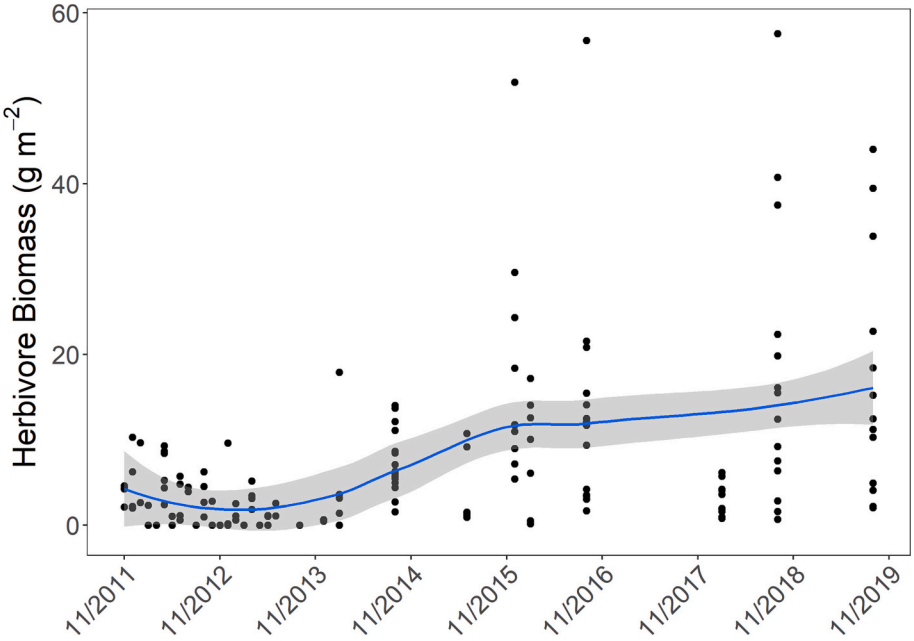

Fig. 5. Herbivore biomass (g m^{-2}) over time fit using a loess smoother, with points representing survey (transect) level observations.

climb through the rest of the survey period with a mean of 16.6 g m^{-2} in 2019 across all reefs surveyed. Visualizing herbivore functional groups alongside E/K cover using nMDS revealed a strong negative relationship between the biomass of herbivorous fish functional groups and E/K cover (Fig. 6). RDA revealed a significant effect of both browsers ($p = 0.039$) and grazers ($p = 0.001$); surveys with low E/K cover were correlated with higher biomass of each of these functional groups (adjusted $R^2 = 0.37$).

In addition to herbivore biomass, live coral cover, SST, wind speed, and rainfall were also significantly associated with E/K cover (Fig. 4). Sea surface temperature and wind speed both exhibited non-linear, monotonic relationships with E/K cover, while live coral cover and rainfall appeared to follow a non-linear, non-monotonic relationship with E/K. Overall, live coral cover, SST, rainfall, and herbivore biomass were higher in years following the E/K decline (2017–2018) than in prior years (2011−2012); wind speed was lower (Fig. 7). We also found that E/K cover associated with management treatment was significantly lower than E/K cover when management was absent (Fig. 4).

4. Discussion

After the introduction of E/K in Kāne'ohe Bay in the 1970s, the invasive algae rapidly spread throughout the bay and remained in relatively high abundance until a substantial decline began in 2013. Rather than a single environmental pulse event dramatically reducing or eliminating E/K throughout the bay in a short time period, our results suggest the decline in Kāne'ohe Bay was gradual and driven by several potential processes. The decrease in E/K cover over the study period varied across reefs, yet was strongly correlated with herbivore biomass, coral cover, SST, wind speed, and rainfall.

Herbivore biomass emerged as a significant driver of E/K decline over time in Kāne'ohe Bay. Herbivorous reef fish span across several functional groups, each with varying behavior and morphology that serve complementary roles in maintaining the health of coral reef ecosystems by contributing to the balance between coral and algal dominance (Bellwood et al., 2004; Adjeroud et al., 2009; Burkepile and Hay, 2010; Adam et al., 2011). Browsers play a crucial role in reducing macroalgae on coral reefs, as they consistently feed on macroalgae and associated epiphytic material (Green and Bellwood, 2009). In Kāne'ohe Bay, sites with low E/K cover were strongly correlated with high biomass of browsers, such as *Naso unicornis* and *Kyphosus* spp., suggesting that these herbivorous fishes assisted in the reversal of the coral-macroalgal phase shift across the studied patch reefs. Gut content analysis of reef fish in Kāne'ohe Bay demonstrated that invasive macroalgae have been a substantial component of the diets of herbivorous reef fish, particularly that of the native browser *N. unicornis* (Stamoulis et al., 2017). Certain species of herbivorous fish even prefer invasive macroalgae over native algal species in Hawai'i (Vermeij et al., 2008). Moreover, management efforts using the native short-spined sea urchin, *Tripneustes gratilla*, as a biocontrol agent have been effective in Kāne'ohe Bay; these generalist herbivores have been documented to feed on multiple species of invasive algae (Neilson et al., 2018; Stimson et al., 2007; Westbrook et al., 2015).

Our findings are consistent with the results of grazing experimental work done in 2014 by Stimson and Larned (2021), in which native herbivorous fish were demonstrated to reduce the abundance of invasive macroalgae in Kāne'ohe Bay. Fish grazing intensity surpassed that of algal growth on both reef flats and reef slopes of patch reefs (Stimson and Larned, 2021). We observed a significant increase in herbivore biomass over the study period that corroborates findings from Stimson and Larned (2021), who documented a positive change in the density and abundance of herbivorous fishes in Kāne'ohe Bay from 2007 to 2014 (Stimson and Larned, 2021). While precise drivers of the increase in herbivorous fishes in Kāne'ohe Bay over time remain unknown, algal resource abundance has been deemed an important predictor of herbivore biomass (Russ, 2003; Tootell and Steele, 2016). The increase also coincides with a large recruitment event of reef fishes in the summer of 2015 (*pers obs*), which may have contributed to the increasing biomass in the years following as that cohort grew larger. The peak in herbivore biomass, which did not occur until several years after the peak in E/K cover, could have resulted from new, small-bodied herbivore recruits that potentially benefited from the high food availability, facilitating their survival and growth to larger sizes in subsequent years when they were better detected during surveys and biomass accumulated. There is also a potential tipping point in herbivory that helped to both reduce E/K cover and also to maintain its abundance at low levels. The relationship between macroalgae and herbivory on coral reefs has been well documented to be non-linear (Graham et al., 2015), with tipping points that lead to macroalgal dominance on reefs demonstrated to fall below the range of ambient herbivory (Holbrook et al., 2016). With herbivores increasing in biomass over time in Kāne'ohe Bay, a threshold level of herbivory may have reached here by 2016 that could explain how E/K cover remained suppressed after the initial decline. While invasive species of macroalgae persist in Kāne'ohe Bay today, cover is low and largely reduced to tight crevices, suggesting that growth remains partly in check from herbivores (Fig. 1). Herbivorous fish in Kāne'ohe Bay have been documented to exhibit high site fidelity, so area specific fisheries management tools may be particularly useful in maintaining herbivore

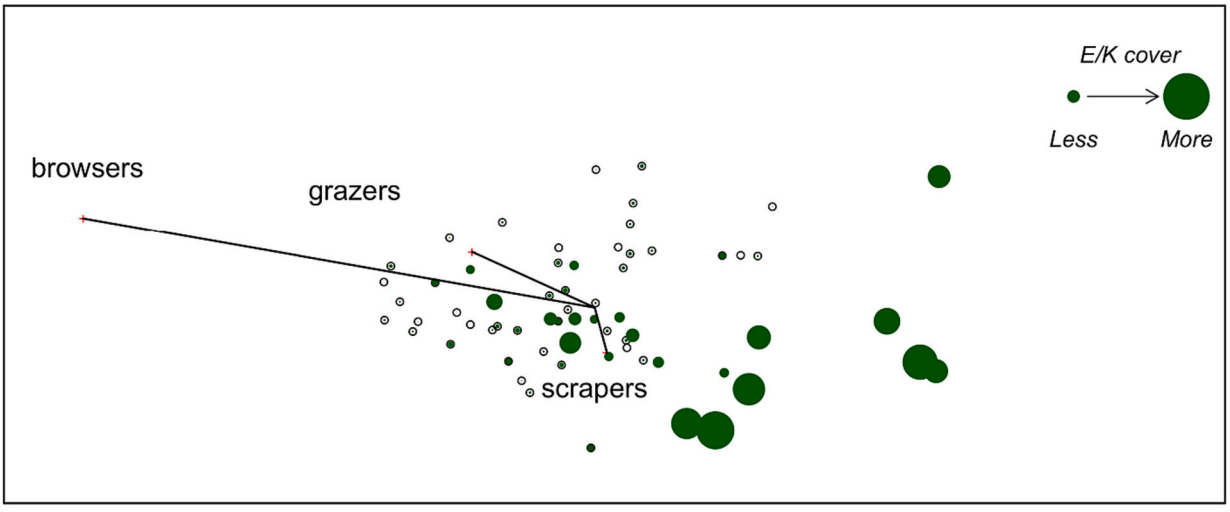

Fig. 6. Non-metric multidimensional scaling plot of herbivore functional groups biomass with vectors corresponding to each of the three groups, and the size of points corresponding to E/K percent (%) cover.

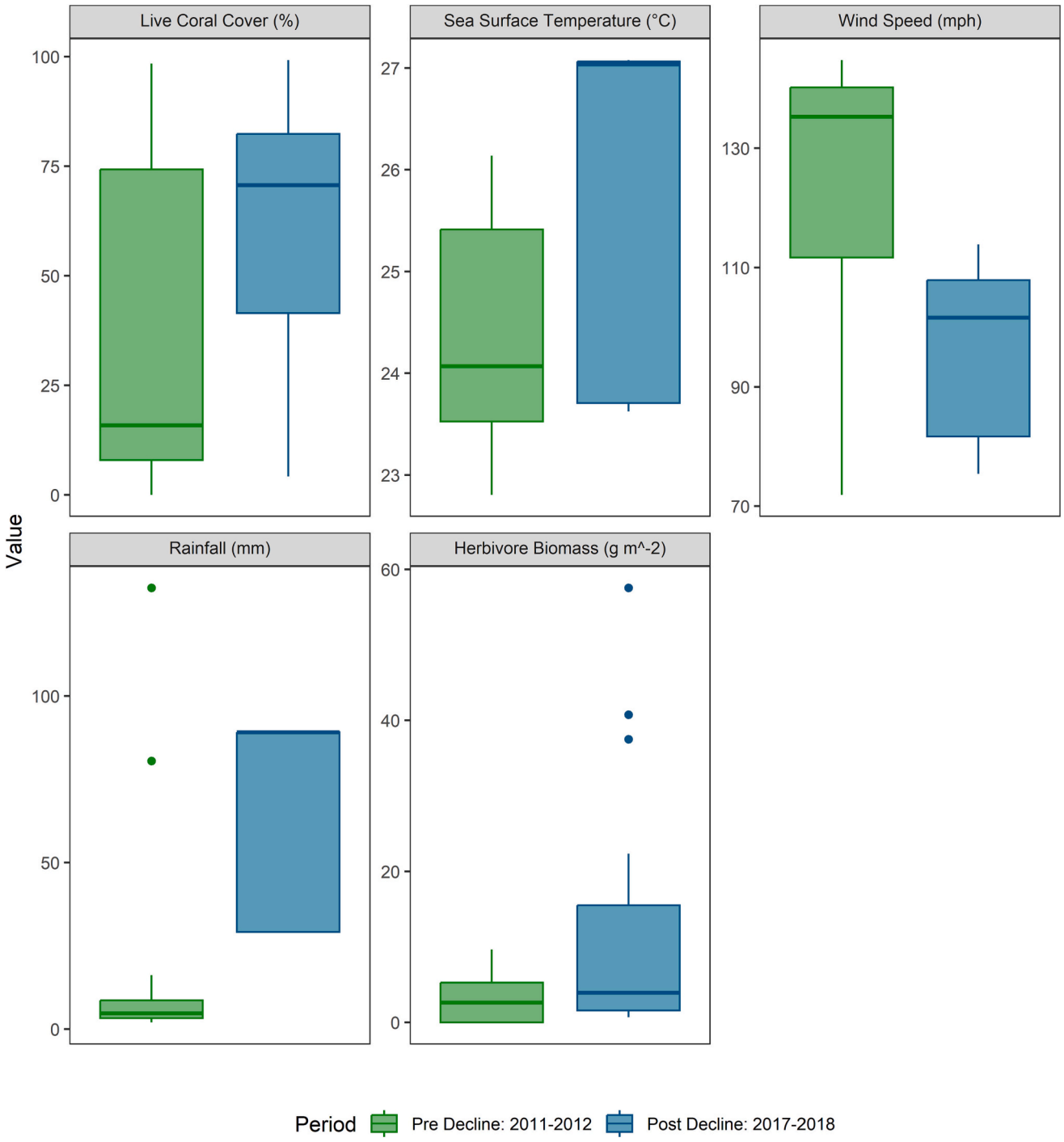

Fig. 7. Boxplots of significant environmental correlates to E/K percent cover, with values pre- (2011–2012) and post (2017–2018) decline.

populations at high enough levels to keep invasive algae in check (Game et al., 2009; Williams et al., 2016; Stamoulis et al., 2017; Chung et al., 2019).

Live coral cover was also significantly correlated with E/K cover in Kāne'ohe Bay over the survey period and may have increased as a result of the E/K decline, or due to extrinsic environmental factors that also contributed to the change in E/K cover. Despite chronic anthropogenic impacts to Kāne'ohe Bay, coral communities have displayed remarkable recovery potential over several decades (Bahr et al., 2017). As E/K declined overall from 2011 to 2019, coral cover at the surveyed reefs ultimately remained stable despite the severe coral bleaching events of 2014 and 2015. Previous work has documented corals capable of outcompeting algae and recovering quickly post bleaching (Diaz-Pulido et al., 2009). Armed with their own defense mechanisms (Nugues and Bak, 2006), coral can prevent algae overgrowth (Diaz-Pulido and McCook, 2004) and even overgrow colonizing algae (Bak et al., 1977; Meesters and Bak, 1994; Diaz-Pulido et al., 2009). Moreover, during mitigation efforts when algae was manually removed in Kāne'ohe Bay, live coral was observed under dense algal mats that had previously concealed their presence (Neilson, *pers. obs*) and thus the rapid recovery of coral cover after E/K declines may be attributable in part to these surviving corals. Whether these specific mechanisms were at play are unknown, but the persistence and recovery of coral cover on reefs that were previously dominated by E/K is another case of the remarkable

resilience of Kāne'ohe Bay corals to disturbance.

Variability in salinity across space has resulted in discrete benthic communities (La Valle et al., 2021), with sudden changes in salinity linked to mortality of coral and ultimate coral community restructuring (Porter et al., 1999; True, 2012). E/K has also been documented to be sensitive to changes in salinity; levels of <20 ppt were shown to be lethal (Largo et al., 1995); therefore, we hypothesized that freshwater influx into the bay may have contributed to the decline of invasive macroalgae. In July of 2014, a major flash flood occurred due to particularly heavy rainfall. This inundation led to a large decrease in salinity that caused localized mortality of corals and other reef organisms near stream mouths (Bahr et al., 2015). The southern reefs of Kāne'ohe Bay, where the majority of this study's surveys were conducted, are particularly vulnerable to freshwater input from the He'eia stream and triple mākāhā (sluice gate) within Paepae o He'eia (Möhlenkamp et al., 2019). Similarly, the 2006 decline of the invasive algae *Dictosphaeria cavernosa*, which had previously dominated reefs in Kāne'ohe Bay, has been linked to the impacts of an exceptionally rainy period spanning 42 days (Stimson and Conklin, 2008). However, the non-monotonic relationship between rainfall and E/K cover suggests rainfall may still benefit E/K growth up to a certain threshold. Nutrient enrichment linked to rainfall may be a contributing factor, as has been documented to contribute to the proliferation of macroalgae in coral reefs worldwide (den Haan et al., 2016; Fong et al., 2020; Adam et al., 2021).

During the survey period, reefs in Kāne'ohe Bay experienced elevated sea surface temperatures (SST) that were associated with three coral bleaching events (2014, 2015, and 2019) (Fig. 7, Rodgers et al., 2017; Winston et al., 2022). However, the initial reduction in E/K cover in Kāne'ohe Bay began prior to the 2014 bleaching event, and Degree Heating Weeks (a common proxy used to describe the magnitude of heat stress) did not emerge as significant predictor. This coupled with the overall positive relationship between E/K and SST predicted by the GAMM, suggests that it is less likely that the heat stress events played a strong role in moderating E/K cover. As temperature plays a role in regulating the metabolic rates and subsequent caloric requirements of organisms, the higher SST recorded during the thermal anomalies could have indirectly influenced a decrease in E/K by increasing grazing rates of herbivores (Clarke and Johnston, 1999; Smith, 2008).

This study highlights the underlying importance of spatial variability in abiotic and biotic factors across patch reefs in Kāne'ohe Bay. While several environmental drivers emerged as significant in explaining temporal patterns of E/K abundance, these measures were obtained from a single established monitoring station at Moku o Lo'e, and were thus not spatially explicit. Herbivore biomass and coral cover were spatially explicit, with surveys associated with each reef and year included in our study. Unfortunately, no other reef-scale environmental or ecological data were available across our entire survey effort timeline. Thus, matching the spatial and temporal scales of E/K cover with the measurements of drivers is a limitation that should be taken into account when interpreting this study's results, and supports the collection of more spatially explicit environmental driver data for future investigations. We also acknowledge that a two-tiered invasive macroalgae control approach was taking place during the study period, further differentiating the fate of one reef from another. Previous work by Neilson et al. (2018) showed the successful management of E/K on patch reefs in Kāne'ohe Bay, which we accounted for by including management treatment as a fixed effect in our models. While manual removal of macroalgae and urchin biocontrol measures reduced E/K cover by 85 % from 2011 to 2013, cover had declined at both treatment and control reefs by the summer of 2013 (Neilson et al., 2018), corresponding to the beginning period of the decline observed in this study. However, treatment still emerged as a significant effect in our model, supporting the utility of management actions to reduce invasive macroalgae in in Kāne'ohe Bay in the context of other drivers of E/K abundance.

Macroalgal proliferation, driven by eutrophication and declining herbivory, is amongst the many threats faced by reefs that together with the increasing impacts of climate change are contributing to the loss of live coral worldwide (Pandolfi et al., 2003; De'Ath et al., 2012; Donovan et al., 2021). If the growth of macroalgae is left unchecked, the resulting collapse of coral reefs will take with it an array of important ecosystem services including but not limited to seafood production, shoreline protection, habitat provision, medicine materials, and nitrogen fixation (Moberg and Folke, 1999). While E/K cover has remained low and nearly absent from many patch reefs in Kāne'ohe Bay since 2015, a slight increase from 2019 on has been observed at some reefs. Monitoring of reefs in Kāne'ohe Bay should continue in the future to detect further warning signs of invasive algae blooms. The role of herbivorous fish and potential influence of episodic freshwater inundation in driving the decline of E/K emphasizes the importance of herbivore and watershed management. Spatial management elsewhere in Hawai'i has resulted in higher standing stocks of herbivorous fish and subsequent declines in macroalgal cover (Friedlander et al., 2007; Williams et al., 2016). While coral reef ecosystems are in decline around the world, Kāne'ohe Bay has surprisingly retained high coral cover over the past several decades, with corals demonstrating remarkable abilities to both acclimatize to increasing stressors and recover following substantial disturbance events (Barnhill and Bahr, 2019). This resilient reef system may offer a bright spot of hope in a future increasingly dominated by doom and gloom for coral reefs.

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CRediT authorship contribution statement

Morgan Winston: Conceptualization, Methodology, Software, Formal analysis, Investigation, Data curation, Writing – original draft, Writing – review & editing, Visualization. **Kimberly Fuller:** Investigation, Resources, Data curation, Writing – review & editing. **Brian J. Neilson:** Conceptualization, Methodology, Investigation, Resources, Data curation, Writing – review & editing, Funding acquisition, Supervision, Project administration. **Mary K. Donovan:** Methodology, Software, Formal analysis, Writing – original draft, Writing – review & editing, Visualization, Conceptualization, Funding acquisition, Supervision, Project administration.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data and code are available on GitHub, and a repository link is provided in the manuscript.

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Appendix A. Supplementary data

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