



Benthic foraminifera as bioindicators for assessing reef condition in Kāneʻohe Bay, Oʻahu, Hawaiʻi

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ABSTRACT

Context. Tropical coral reef environments provide a wide variety of goods and ecosystem services but are experiencing growing pressure from coastal development and tourism. Assessing the status of reef communities along gradients of human pressure is therefore necessary to predict recovery and resilience capacity of reefs. **Aims.** First, to determine the overall water quality in Kāneʻohe Bay, Oʻahu, Hawaiʻi, by employing a low-cost monitoring approach for anthropogenic stress on coral reef areas. Second, to assess the suitability of the monitoring approach to complement existing monitoring programmes. **Methods.** Sediment samples containing benthic foraminifera were used to determine water quality and stressor sources in Kāneʻohe Bay, Oʻahu, Hawaiʻi, by applying the Foram Index (FI) and Bayesian regression analysis. The FI is based on relative abundance of functional groups of larger benthic foraminifera. **Key results.** Overall water quality in Kāneʻohe Bay may support active growth and recovery of coral reefs in the northern sector but deteriorates around Kāneʻohe City. **Conclusions.** Benthic foraminifera can be used as bio-indicators in Hawaiian reefs, providing an easy and fast-to-apply method for assessing short-term changes in water quality and stress sources. Implementing benthic foraminifera studies within existing long-term monitoring programs of Hawaiian reefs can be beneficial for conservation efforts. **Implications.** Within a historic context, our findings illustrate the modest recovery of an ecosystem following pollution control measures but highlight the need of conservation efforts for reef environments adjacent to major human settlements.

Keywords: anthropogenic stress, assessment, coral reef, corals, foram index, marine, monitoring, pollution, reef crisis, reef health, water quality.

Introduction

Coral reef environments provide a wide variety of goods and services, including waste detoxification and vital food resources for millions of people (Holmlund and Hammer 1999; Adger *et al.* 2005; Woodhead *et al.* 2019). However, current climate warming, the increase of ocean pollution, acidification of the oceans, and the manifold forms of habitat destruction endanger modern coral reefs (Pandolfi *et al.* 2003; Barnosky *et al.* 2017). To evaluate and subsequently manage coral reef ecosystems, reefal, ecological, environmental, and anthropogenic characteristics must be considered (Sandin *et al.* 2008). Anthropogenic impacts in particular are a growing threat to coral environments, as the population of the Earth is projected to increase dramatically in the next 35 years (Dubois 2011). Coral reef environments on the Hawaiian Archipelago represent one of the most intensively studied reef systems worldwide, with an exceptional record of both natural and human-induced perturbations of the past. Coral reef ecosystems on Hawaiʻi experienced major bleaching events (Burke *et al.* 2011) as well as rapid sea level rise (Leuliette 2012) and were subject of major anthropogenic impacts (Williams *et al.* 2008; Filous *et al.* 2017; Friedlander *et al.* 2018). Anthropogenic stressors on Hawaiʻi likely have amplified in the past decades, as coastal development continues to increase with a growing human population. Current long-term monitoring programs focus mainly on the description of spatial and temporal

dynamics of Hawaiian reef communities, and less on the potential anthropogenic drivers of these dynamics (Jokiel *et al.* 2004; Rodgers *et al.* 2015).

Here, we employ a low-cost approach to monitor anthropogenic stress on coral reef areas on Hawai'i and assess its suitability to complement existing monitoring programs. The methodological approach was initially developed for western Atlantic-Caribbean reefs (Hallock *et al.* 2003) but has since been successfully extended to reefal areas all over the world (Hallock 2012). We first report the abundance and distribution of benthic foraminifera genera from 13 sediment samples in Kāne'ohe Bay, Hawai'i. As assemblages of benthic foraminiferal shells in sediment closely reflect water and sediment quality, they can be used to monitor high-resolution records of coastal pollution (Hallock *et al.* 2003; Frontalini and Coccioni 2008; Uthicke and Nobes 2008) and anthropogenic stress (Alve 1991; Frontalini and Coccioni 2008; Caruso *et al.* 2011). To do so, we transformed the raw abundance counts of foraminiferal shells into a well-established measure for water quality, the Foramin Index (FI) (Hallock *et al.* 2003; Hallock 2012; Prazeres *et al.* 2020). The FI is based on the ratio of three functional groups of foraminifera: (1) taxa of larger foraminifera that host algal symbionts and reflect high water quality; (2) pollution-tolerant opportunistic foraminifera that dominate high-stress environments; and (3) small taxa that proliferate in response to eutrophication. We then used

the FI and distances to potential centres of anthropogenic stress (Kāne'ohe City, Kahalu'u City, and the Marine Corps Base Hawai'i) to analyse whether spatial assemblage shifts are correlated with anthropogenic impacts in Kāne'ohe Bay. Our results indicate that overall water quality is high in Kāne'ohe Bay but deteriorates around Kāne'ohe City. Given the potential applicability and a low expenditure of foraminiferal-based measures for water quality, we propose that implementing benthic foraminifera as bio-indicators for Hawaiian reefs can be beneficial for existing long-term monitoring programs.

Materials and methods

Regional setting

Kāne'ohe Bay, situated on the windward coast of O'ahu, Hawai'i, is one of the most intensely studied estuarine and coral reef systems in the world (Bathen 1968; Banner 1974; Hunter and Evans 1995). It is located on the north-east coast of O'ahu with a length of 13.5 km at its maximum and 4.5 km width from shore to the outer barrier reef (Fig. 1). The bay is bordered by the only barrier reef in the Hawaiian archipelago. The reef is cut by two natural channels and a dredged ship channel connecting the north and the south passages. Between the 1940s and 1970s, Kāne'ohe Bay coral reefs suffered impacts to the reef

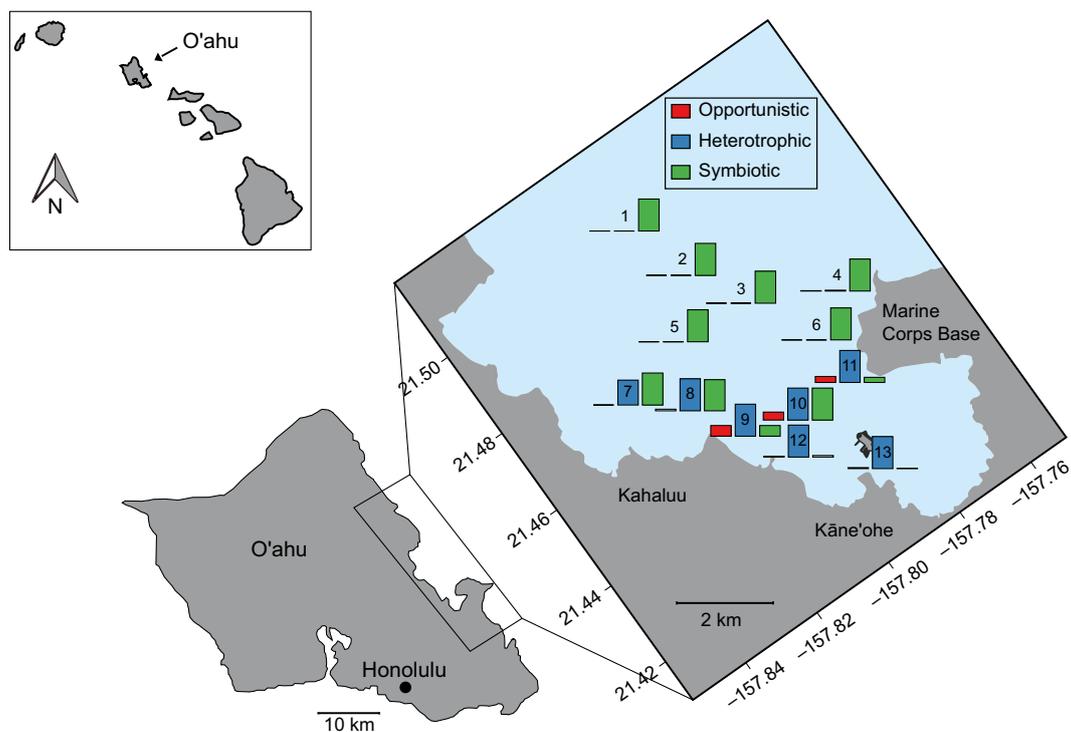


Fig. 1. Location map of Kāne'ohe Bay, O'ahu, Hawai'i, showing the proportional foraminiferal distribution at the sampled sites. Green, symbiont-bearing genera; blue, heterotrophic genera; and red, opportunistic genera.

community due to anthropogenic activities concomitant with land use changes, such as eutrophic conditions ensuing from sewage discharges into the bay, and channelisation of streams (Pastorok and Bilyard 1985; Ringuet and Mackenzie 2005). Additionally, extensive reef dredging amplified these impacts. Two large sewage outfalls were diverted from the bay in 1977–1978 (Smith *et al.* 1981; Laws and Redalje 1982), followed by a partial recovery of coral-reef dominated communities in Kāneʻohe Bay (Hunter and Evans 1995). This trend, however, was slowing down since 1984 and subsequently even reversed, co-occurring with increasing size of the adjacent cities Kāneʻohe and Kahaluʻu and the expansion of the marine corps-base (Hunter and Evans 1995). This urban growth concurred with non-point source pollution as well as increased runoff nutrient input into the bay linked to considerable impacts on the bay ecosystem (Ringuet and Mackenzie 2005; Hoover *et al.* 2006). Foraminiferal assemblages responded to these perturbations with a shift in composition and a severe decrease in abundance (P. Hallock, pers. comm.). Kāneʻohe Bay is monitored since 1999 as part of the Hawaiʻi Coral Reef Assessment and Monitoring Program. Between 1999 and 2002, coral reef coverage decreased in five out of six sampled stations in Kāneʻohe Bay (Jokiel *et al.* 2004), whereas only one of the six stations showed a decrease over a 14-year period (Rodgers *et al.* 2015).

Sampling sites

Samples were collected during 2017 from Kāneʻohe Bay by researchers from the Florida Museum of Natural History sampling surface sediment by scuba diving. Thirteen samples were taken across a variety of shallow water environments between 1 and 14 m water depth and a variety of distances from settlements on the island to examine the spatial variation in assemblage and any potential impact from anthropogenic sources (Supplementary Table S1). The locality in the bay, the longitude and latitude, the water depth, and the habitat were assigned to each individual sample. The distance to centres of anthropogenic stress (cities and military bases) were calculated by using the programme Google Earth (<http://earth.google.com>).

Sampling treatment

The foraminiferal assemblages were wet sieved through 63 μm and dried in a low temperature oven ($\sim 40^\circ\text{C}$). Following this, up to 200 foraminiferal specimens of each sample were picked under a stereo microscope following a standard protocol (Hallock *et al.* 2003). Each sample was split into smaller subsets of approximately 0.1 g and weighed. We then used the first weighed subset of the sample to pick out foraminiferal specimen until we reached a number of 200 specimen (Dix 2002). If less than 200 specimen were present in the subset, we repeated the

picking procedure on a second 0.1 g subset from the sample. This procedure was repeated until 200 specimens were obtained or until the entire gram of sample was processed. Foraminiferal taxa were identified to generic level according to Loeblich and Tappan (2015). We used the FI (Hallock *et al.* 2003; Hallock 2012; Prazeres *et al.* 2020) to assess water quality and suitability for reef-building corals of the study area. The FI is defined by the ratio of large benthic foraminifera that host phototrophic endosymbionts to small heterotrophic foraminifera. Heterotrophic taxa proliferate under the input of nutrients into the sea water, while large symbiont-bearing taxa are constrained to water-quality conditions similar to those required by corals. Under extreme local nutrient input, with subsequent intermittent anoxia in the sediments, a few known taxa of heterotrophic, stress-tolerant foraminifera can become dominant (Alve and Bernhard 1995; Carnahan *et al.* 2009; Pisapia *et al.* 2017). Accordingly, we classified specimens into one of three functional groups: (1) symbiont-bearing; (2) opportunistic; or (3) other smaller taxa. For each sample, the FI was determined by the equation: $FI = (10 \times P_s) + (P_o) + (2 \times P_h)$, where 'P' is the proportion and where subscript 's' represents symbiont-bearing foraminifera, subscript 'o' represents opportunistic foraminifera, and subscript 'h' represents other small, heterotrophic foraminifera. The FI scale ranges from 1 to 10, with $FI > 4$ indicating environment conducive to reef growth, $2 < FI < 4$ indicating environment marginal for reef growth and unsuitable for recovery, and $FI < 2$ indicating stressed conditions unsuitable for reef growth. During specimen counting, the degree of bioclast preservation was also evaluated (Carnahan *et al.* 2009; Hallock 2012). Badly broken or possibly reworked specimen, which could not be identified to genus level, were omitted from the analysis (Hallock *et al.* 2003; Prazeres *et al.* 2020). Relative abundance (proportions of the subsample) and absolute abundance (numbers of specimens per gram of sediment) were calculated following standard procedures (Hallock *et al.* 2003).

Data analysis

All analysis were carried out using the R programming environment (R Core Team 2021). We used the 'tidyverse' package collection for data wrangling and visualisation (Wickham *et al.* 2019), the 'vegan' package (Oksanen *et al.* 2020) for non-metric multidimensional scaling (nMDS) ordination, and the 'brms' package for Bayesian regression analysis (Bürkner 2017). nMDS was conducted to analyse the community structure of all samples and was based on Bray-Curtis dissimilarity. Bayesian linear regression analysis was carried out to test if the water quality as indicated by the FI in the southern area of Kāneʻohe Bay, which is mainly characterised by urban development, is lower compared to the northern sector, which is further away from cities and

military bases. We first fitted three regression models with the FI as the outcome variable including an intercept only null model, a model with distances to all major human settlements in the bay (Kāneʻohe City, Kahaluʻu City, and Marine Corps Base Hawaiʻi (MCBH), and a model with all settlements and additionally water depth as a predictor variable. This approach enabled us to compare the predictive effect of distance to human settlements to a null baseline as well as to water depth, which might be a possible confounding driver of the FI (Hallock 2012). Models were compared by means of leave-one-out cross-validation using Pareto-smoothed importance sampling (Vehtari *et al.* 2017). We transformed the outcome and all predictor variables to z-scores prior to model fitting to facilitate an easier calculation of the joint posterior probability distribution. All three models were fitted via the probabilistic programming language Stan using a Hamiltonian Monte Carlo Markov Chain (MCMC) and the No-U-Turn sampler (Gelman *et al.* 2015). We used weakly informative priors for all parameters that were easily exceeded by the actual data while reducing over-fitting compared to traditional frequentist approaches. The joint posterior probability distribution was estimated by four MCMC chains, a warm-up of 500 samples, and 2000 actual samples. We then used standard convergence and efficiency diagnostics to evaluate the sampling performance, based on Rhat values and the number of effective sample size (Vehtari *et al.* 2021).

Robustness testing

As a FI value of 10 is possible but unusual even in pristine regions (see Discussion), we further conducted a robustness test by removing all samples with values above 9.5 and

repeating our analysis on this data subset. We then compared the results from the analysis based on the subset to the results based on all samples, to see whether potentially biased samples with FI values above 9.5 might confound our findings.

Results

Community analysis

The assemblages show an average generic level-richness compared to other tropical warm water coral reefs (Hallock 2012). In total, 15 genera were identified and classified according to the three functional groups: (1) symbiont-bearing; (2) opportunistic; and (3) small heterotrophic foraminifera (Table 1). A clear spatial distribution of foraminiferal assemblages Kāneʻohe Bay can be perceived: The northern sector is dominated by symbiont-bearing genera, in the middle sector all three functional groups are present, and the southern sector is characterised by heterotrophic genera (Fig. 1). Sample sites located on the barrier reef (1–6) are all dominated by symbiont-bearing foraminifera. In the middle sector of the bay, between the barrier reef and the coastline, the number of small heterotrophic genera increases. While the four samples that are located closest to the shore (9, 11–13) are dominated by small heterotrophic genera, the three samples in the middle sector (7, 8, 10) show an equal distribution between heterotrophic and symbiont-bearing taxa. Opportunistic genera are most abundant in the middle sector; however, they still remain the least abundant of the three functional groups even in the middle sector. Symbiont-bearing and opportunistic taxa are less abundant in the four near-shore

Table 1. Relative abundance of the main foraminiferal groups and absolute abundance of foraminifera in Kāneʻohe Bay, Oʻahu, Hawaiʻi.

Sample	Symbiont-bearing					Other small taxa	Opportunistic				Absolute abundance
	<i>Amphistegina</i>	<i>Heterostegina</i>	<i>Peneroplis</i>	<i>Alveolinida</i>	<i>Soritida</i>		<i>Ammonia</i>	<i>Textulariida</i>	<i>Bolivinida</i>	<i>Elphidium</i>	
1	91	2.5	1.5	2	2.5	0.5	0	0	0	0	50
2	93	4	0	0	1	2	0	0	0	0	7.2
3	74.2	0	13.6	0	12.1	0	0	0	0	0	3.3
4	46.5	17.5	28	0	4.5	2.5	0.5	0	0	0.5	20
5	96.8	0	1.2	0	0	1	1	0	0	0	4.2
6	87.5	4.2	2.1	0	6.3	0	0	0	0	0	2.4
7	0	0	25	0	31.3	43.8	0	0	0	0	1.6
8	0	0	24.1	0	24.1	49.4	2.4	0	0	0	4.2
9	0	0	0	0	20	60	0	0	20	0	1
10	0	0	11.1	0	33.3	44.4	0	0	11.1	0	0.9
11	3.5	0	7.5	0	1	74	14	0	0	0	40
12	0	0	3.5	0	1	93	2	0.5	0	0	133.3
13	0	0	1	0	0	94	1.5	0.5	1	0	100

Relative abundance is shown in percentage and absolute abundance in number of specimen per gram sediment.

samples. Overall, absolute abundance ranged from 0.9 to 133.3 individuals per gram of sediment, including three samples with less than two specimen per gram of sediment. The most abundant genera of the symbiont-bearing functional group were *Amphistegina* spp., *Peneroplis* spp., *Sorites* spp. and *Heterostegina* spp. (see Table S1 for relative and absolute abundance of all foraminiferal taxa). Opportunistic species were generally rare, and included *Ammonia* spp., *Elphidium* spp., and *Bolivina* spp. The genus *Amphistegina* spp. from the symbiont bearing group had the greatest relative abundance. It dominated 46% of the assemblages, whereas the other 54% were dominated by small heterotrophic group genera. *Amphistegina* spp. also constituted 38% of the total foraminiferal population in Kāneʻohe Bay and was present in 7 of the 13 sampling stations. However, *Peneroplis* spp. and *Sorites* spp. were found in 11 of the 13 sampling stations, making them the most widespread genera. Non-metric multidimensional scaling based on the foraminiferal assemblages show a clear clustering of the samples in three groups, closely corresponding to the three functional groups used to calculate the FI (Fig. S3).

Foram Index (FI)

The FI calculated for the sampled sites revealed values between 2.1 and 10, with a median of 6.8 (Fig. S1, Table S2). Four samples (9, 11–13, located close to the shore) are

indicating environment marginal for reef growth and unsuitable for recovery, whereas the remaining nine samples are indicating environment conducive to reef growth. FI results mirror assemblage clusters attained by applying a nMDS scaling approach to the samples, indicating a strong biotic driver for foraminiferal distribution and emphasising the reliability of the FI.

Distance to human settlements

Model comparison showed that distance to human settlements (Kāneʻohe City, Kahaluʻu City, and MCBH) is a robust predictor of the FI (Table S3). The Bayesian regression model revealed a substantial relationship between FI values and distance to Kāneʻohe City, showing that samples scored lower FI values when they were located closer to Kāneʻohe City (Figs 2 and 3). The model yielded no robust relationships between FI values and distance to Kahaluʻu City and MCBH, respectively. A regression model fitted on a subset of the data for robustness testing (see Materials and Methods and Fig. S2) yielded similar results, with a strong relationship between the FI and distance to Kāneʻohe City while showing no consistent relationship for distance to Kahaluʻu City and to the MCBH. Our results hence indicate that a stress gradient is present in Kāneʻohe Bay, with the highest stress close to Kāneʻohe City and less further away from Kāneʻohe City, while smaller settlements in the bay have less to no impact.

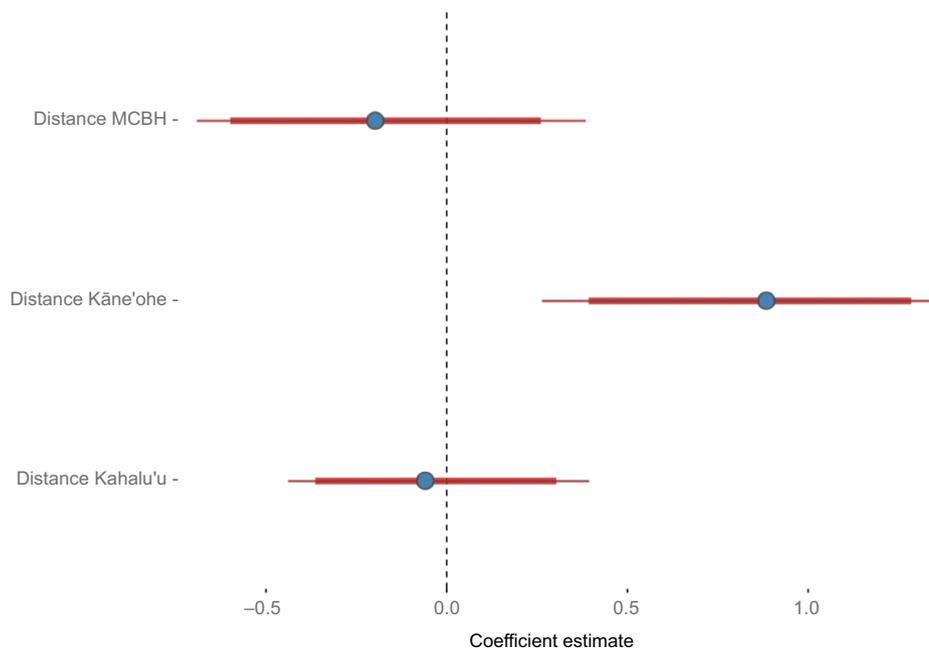


Fig. 2. Coefficient plot for the effect of the distance to major human settlements in Kāneʻohe Bay on the Foram Index, as a result of a Bayesian linear regression. The dashed line depicts an effect of zero. Red lines show credible intervals, with the thicker line showing the range of the 89% interval, and the finer line the 95% interval. Points show the median of the focal joint posterior distribution. MCBH, Marine Corps Base Hawaiʻi.

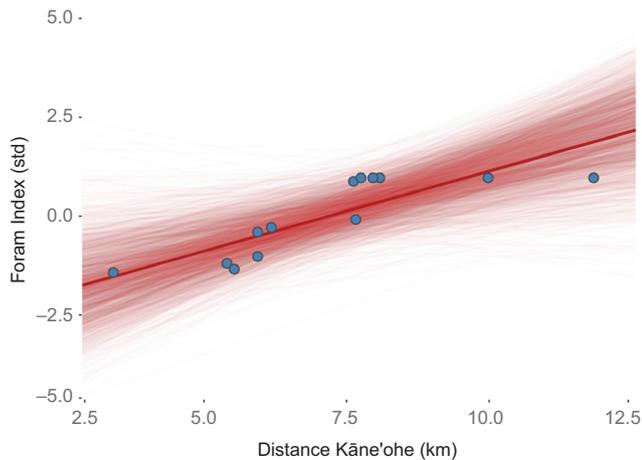


Fig. 3. The effect of distance to Kāneʻohe City on the standardised Foram Index as estimated by a Bayesian linear regression. Blue points show the actual sediment samples. The thick red line depicts the median trend line for the relationship between the distance and the Foram Index. Thinner red lines show trend lines from 2000 samples from the joint posterior to visualise uncertainty around the median trend line.

Discussion

Using a foraminiferal-based index for water quality, we found a clear spatial stress gradient in Kāneʻohe Bay with good water quality in the outer bay and low water quality close to the shore. The distance of each sediment sample to Kāneʻohe City turned out to be a strong predictor of this trend, while smaller settlements in the bay seemed to be less influential. This effect might result from non-point pollution by the adjacent city of Kāneʻohe, or by organic matter input through the river mouths in this area. Our results are in line with other empirical studies showing periodical reef degradation in Kāneʻohe Bay either through anthropogenic activities or natural processes such as freshwater flooding and erosional runoff (Hunter and Evans 1995; Laws and Allen 1996; Jokiel and Brown 2004; Neilson 2014). We further found the majority of the sampled area conducive to reef growth. One reason for these moderate to good conditions for coral reefs could be that the water body of Kāneʻohe Bay is relatively well mixed vertically and horizontally under most conditions (Ringuet and Mackenzie 2005). Possible pollution sources around Kāneʻohe are therefore quickly dispersed, as well as organic matter from riverine input. However, one-third of our samples indicated environment marginal for reef growth and unsuitable for recovery. This might be particularly warning as major coral bleaching events were observed in Kāneʻohe Bay in the past (Jokiel and Brown 2004; Neilson 2014). Hence, reefs close to the shore and especially close to Kāneʻohe City might not be able to recover after a period of perturbations, be it natural or anthropogenic stressors. We therefore agree with

other current reef health assessments of Kāneʻohe Bay that it is necessary to pay continuous attention to local pollution, impacts of climate change, sedimentation, and harvest issues (Jokiel *et al.* 2004; Bahr *et al.* 2015; Rodgers *et al.* 2015). Ongoing monitoring programs in the bay could benefit from the implementation of the FI as a fast and low expenditure method to assess conditions for reef growth. Although this index was not specifically developed for use in islands in the central Pacific Ocean (Hallock *et al.* 2003), our study shows that the application to Hawaiian reefs is feasible as our results are in line with other studies in Kāneʻohe Bay using a variety of indicators for reef health and water quality (Maragos 1972; Hunter and Evans 1995; Fagan and Mackenzie 2007; Rodgers *et al.* 2015; Friedlander *et al.* 2018).

FI values obtained in this study appear similar to those from other regions with anthropogenic pollution (Barbosa *et al.* 2009; Carnahan *et al.* 2009; Caruso *et al.* 2011; Barbosa *et al.* 2012). However, FI values of 10 are seldom recorded in other studies even in pristine regions (Barbosa *et al.* 2009; Barbosa *et al.* 2012). In this study, five samples (1–3, 5, 6) recorded a FI value of approximately 10 in the outer bay of Kāneʻohe, mainly consisting of lens-shaped *Amphistegina* spp. and *Heterostegina* spp. These genera tend to remain in the sediment for a prolonged time due to their test-shape and their robust nature. Hence, samples with a FI of 10 may have experienced reworking by currents for a longer time interval and could be therefore biased. However, these potentially biased samples do not confound our findings, as the robustness testing based on samples 6–13 showed equal results compared to the analysis of all samples. All other samples showed good preservation of delicate test-forms, indicating that the FI from these samples can be considered as reliable and represent accumulation over short time. North-easterly winds present in the northern area (Smith *et al.* 1981; Laws and Allen 1996) might have removed smaller foraminifera taxa from the sediment by grain size sorting, resulting in biased high FI values for this area. However, winter storm motion and trade wind influence is restricted to the northern area (Bathen 1968) and should not influence samples from the southern area. Although the FI can vary with other parameters such as sediment texture (Narayan and Pandolfi 2010), hydrodynamic regime, and light penetration (Barbosa *et al.* 2009), various studies have shown that the FI is primarily related to water quality (Uthicke and Nobes 2008; Koukousioura *et al.* 2011; Velásquez *et al.* 2011; Banner 1974; Oliver *et al.* 2014). The results from our Bayesian regression framework might support this as there was no apparent relationship between the FI and water depth (Table S3). Hence, high FI values of samples 1–5 could be biased by reworking and/or hydrodynamic sorting, but we expect remaining samples to be robust and reflect true water quality. Based on these, the coastal waters adjacent to Kāneʻohe City in the southern

sector seem to be impacted by anthropogenic stress and/or organic material input with eutrophic water conditions.

Based on our results, we emphasise that implementing benthic foraminifera studies within existing long-term monitoring programs of Hawaiian reefs can be beneficial for conservation efforts. We showed that benthic foraminifera can be used as bio-indicators in Hawaiian reefs, providing an easy and fast-to-apply method for assessing short-term changes in water quality and stress sources. Hence, abundance and distribution of benthic foraminiferal taxa reported in this study can be used as a baseline to compare changes in Kāneʻohe Bay over both time and space. In conclusion, we found a clear and robust spatial pattern for reef suitability in Kāneʻohe Bay, with areas closer to the shore and especially closer to Kāneʻohe City being less suitable, while samples from the northern bay area indicated conditions more suitable for reef growth and recovery. Our findings highlight the need of an ongoing monitoring for reef areas in Kāneʻohe Bay to protect the frail local ecosystem from both natural and anthropogenic impacts.

Supplementary material

Supplementary material is available [online](#).

References

- Adger WN, Hughes TP, Folke C, Carpenter SR, Rockström J (2005) Social-ecological resilience to coastal disasters. *Science* **309**, 1036–1039. doi:10.1126/science.1112122
- Alve E (1991) Benthic foraminifera in sediment cores reflecting heavy metal pollution in Sorfjord, western Norway. *The Journal of Foraminiferal Research* **21**, 1–19. doi:10.2113/gsjfr.21.1.1
- Alve E, Bernhard JM (1995) Vertical migratory response of benthic foraminifera to controlled oxygen concentrations in an experimental mesocosm. *Marine Ecology Progress Series* **116**, 137–151. doi:10.3354/meps116137
- Bahr KD, Jokiel PL, Toonen RJ (2015) The unnatural history of Kāneʻohe Bay: coral reef resilience in the face of centuries of anthropogenic impacts. *PeerJ* **3**, e950. doi:10.7717/peerj.950
- Banner AH (1974) Kaneohe Bay, Hawaiʻi: urban pollution and a coral reefs ecosystem. In 'Proceedings of the 2nd International Coral Reef Symposium'. pp. 685–702. (The Great Barrier Reef Committee: Brisbane)
- Barbosa CF, de Freitas Prazeres M, Ferreira BP, Seoane JCS (2009) Foraminiferal assemblage and reef check census in coral reef health monitoring of East Brazilian margin. *Marine Micropaleontology* **73**, 62–69. doi:10.1016/j.marmicro.2009.07.002
- Barbosa CF, Ferreira BP, Seoane JCS, Oliveira-Silva P, Gaspar ALB, Cordeiro RC, Soares-Gomes A (2012) Foraminifer-based coral reef health assessment for southwestern Atlantic offshore archipelagos, Brazil. *The Journal of Foraminiferal Research* **42**, 169–183. doi:10.2113/gsjfr.42.2.169
- Barnosky AD, Hadly EA, Gonzalez P, Head J, Polly PD, Lawing AM, Eronen JT, Ackerly DD, Alex K, Biber E, Blois J, Brashares J, Ceballos G, Davis E, Dietl GP, Dirzo R, Doremus H, Fortelius M, Greene HW, Hellmann J, Hickler T, Jackson ST, Kemp M, Koch PL, Kremen C, Lindsey EL, Looy C, Marshall CR, Mendenhall C, Mulch A, Mychajliw AM, Nowak C, Ramakrishnan U, Schnitzler J, Das Shrestha K, Solari K, Stegner L, Stegner MA, Stenseth NC, Wake MH, Zhang Z (2017) Merging paleobiology with conservation biology to guide the future of terrestrial ecosystems. *Science* **355**, eaah4787. doi:10.1126/science.aah4787
- Bathen KH (1968) 'A descriptive study of the physical oceanography of Kaneohe Bay, Oahu, Hawaiʻi.' (Hawaiʻi Institute of Marine Biology (formerly Hawaiʻi Marine Laboratory))
- Burke L, Reyntar K, Spalding M, Perry A (2011) 'Reefs at risk revisited.' (World Resources Institute)
- Bürkner P-C (2017) brms: an R package for Bayesian multilevel models using Stan. *Journal of Statistical Software* **80**, 1–28. doi:10.18637/jss.v080.i01
- Carnahan EA, Hoare AM, Hallock P, Lidz BH, Reich CD (2009) Foraminiferal assemblages in Biscayne Bay, Florida, USA: responses to urban and agricultural influence in a subtropical estuary. *Marine Pollution Bulletin* **59**, 221–233. doi:10.1016/j.marpolbul.2009.08.008
- Caruso A, Cosentino C, Tranchina L, Brai M (2011) Response of benthic foraminifera to heavy metal contamination in marine sediments (Sicilian coasts, Mediterranean Sea). *Chemistry and Ecology* **27**, 9–30. doi:10.1080/02757540.2010.529076
- Dix TL (2002) The distribution and ecology of benthic foraminifera of Tampa Bay, Florida. PhD dissertation. Department of Marine Science, University of South Florida, Tampa.
- Dubois O (2011) 'The state of the world's land and water resources for food and agriculture: managing systems at risk.' (Earthscan)
- Fagan KE, Mackenzie FT (2007) Air–sea CO₂ exchange in a subtropical estuarine-coral reef system, Kaneohe Bay, Oahu, Hawaiʻi. *Marine Chemistry* **106**, 174–191. doi:10.1016/j.marchem.2007.01.016
- Filous A, Friedlander AM, Koike H, Lammers M, Wong A, Stone K, Sparks RT (2017) Displacement effects of heavy human use on coral reef predators within the Molokini Marine Life Conservation District. *Marine Pollution Bulletin* **121**, 274–281. doi:10.1016/j.marpolbul.2017.06.032
- Friedlander AM, Donovan MK, Stamoulis KA, Williams ID, Brown EK, Conklin EJ, DeMartini EE, Rodgers KS, Sparks RT, Walsh WJ (2018) Human-induced gradients of reef fish declines in the Hawaiian Archipelago viewed through the lens of traditional management boundaries. *Aquatic Conservation: Marine and Freshwater Ecosystems* **28**, 146–157. doi:10.1002/aqc.2832
- Frontalini F, Coccioni R (2008) Benthic foraminifera for heavy metal pollution monitoring: a case study from the central Adriatic Sea coast of Italy. *Estuarine, Coastal and Shelf Science* **76**, 404–417. doi:10.1016/j.ecss.2007.07.024
- Gelman A, Lee D, Guo J (2015) Stan: a probabilistic programming language for Bayesian inference and optimization. *Journal of Educational and Behavioral Statistics* **40**, 530–543. doi:10.3102/1076998615606113
- Hallock P (2012) The FORAM index revisited: uses, challenges, and limitations. In 'Proceedings of the 12th International Coral Reef Symposium, Cairns, Australia'. pp. 9–13. (James Cook University: Townsville, Qld, Australia)
- Hallock P, Lidz BH, Cockey-Burkhard EM, Donnelly KB (2003) Foraminifera as bioindicators in coral reef assessment and monitoring: the FORAM index. *Environmental Monitoring and Assessment* **81**, 221–238. doi:10.1023/A:1021337310386
- Holmlund CM, Hammer M (1999) Ecosystem services generated by fish populations. *Ecological Economics* **29**, 253–268. doi:10.1016/S0921-8009(99)00015-4
- Hoover RS, Hoover D, Miller M, Landry MR, DeCarlo EH, Mackenzie FT (2006) Zooplankton response to storm runoff in a tropical estuary: bottom-up and top-down controls. *Marine Ecology Progress Series* **318**, 187–201. doi:10.3354/meps318187
- Hunter CL, Evans CW (1995) Coral reefs in Kaneohe Bay, Hawaiʻi: two centuries of western influence and two decades of data. *Bulletin of Marine Science* **57**, 501–515.
- Jokiel PL, Brown EK (2004) Global warming, regional trends and inshore environmental conditions influence coral bleaching in Hawaiʻi. *Global Change Biology* **10**, 1627–1641. doi:10.1111/j.1365-2486.2004.00836.x
- Jokiel PL, Brown EK, Friedlander A, Rodgers SK, Smith WR (2004) Hawaiʻi coral reef assessment and monitoring program: spatial patterns and temporal dynamics in reef coral communities. *Pacific Science* **58**, 159–174. doi:10.1353/psc.2004.0018
- Koukousioura O, Dimiza MD, Triantaphyllou MV, Hallock P (2011) Living benthic foraminifera as an environmental proxy in coastal ecosystems: a case study from the Aegean Sea (Greece, NE Mediterranean). *Journal of Marine Systems* **88**, 489–501. doi:10.1016/j.jmarsys.2011.06.004

- Laws EA, Allen CB (1996) Water quality in a subtropical embayment more than a decade after diversion of sewage discharges. *Pacific Science* **50**, 194–210.
- Laws EA, Redalje DG (1982) Sewage diversion effects on the water column of a subtropical estuary. *Marine Environmental Research* **6**, 265–279. doi:10.1016/0141-1136(82)90041-1
- Leuliette EW (2012) 'Sea level trend map. National Oceanic and Atmospheric Administration, Laboratory for Satellite Altimetry sea-level rise products, online data'.
- Loeblich AR Jr, Tappan H (2015) 'Foraminiferal genera and their classification.' (Springer)
- Maragos JE (1972) 'A study of the ecology of Hawaiian reef corals.' (University of Hawai'i)
- Narayan YR, Pandolfi JM (2010) Benthic foraminiferal assemblages from Moreton Bay, South-East Queensland, Australia: applications in monitoring water and substrate quality in subtropical estuarine environments. *Marine Pollution Bulletin* **60**, 2062–2078. doi:10.1016/j.marpolbul.2010.07.012
- Neilson B (2014) Coral bleaching rapid response surveys September–October 2014. Available at <http://dlnr.hawaii.gov/reefresponse/files/2014/10/DARCoralBleachingSrvyResults10.28.2014.pdf>
- Oksanen J, Guillaume Blanchet F, Friendly M, Kindt R, Legendre P, McGinn D, Minchin PR, O'Hara RB, Simpson GL, Solymos P, Henry M, Stevens H, Szoecs E, Wagner H (2020) vegan: community ecology package. Available at <https://CRAN.R-project.org/package=vegan>
- Oliver LM, Fisher WS, Dittmar J, Hallock P, Campbell J, Quarles RL, Harris P, LoBue C (2014) Contrasting responses of coral reef fauna and foraminiferal assemblages to human influence in La Parguera, Puerto Rico. *Marine Environmental Research* **99**, 95–105. doi:10.1016/j.marenvres.2014.04.005
- Pandolfi JM, Bradbury RH, Sala E, Hughes TP, Bjorndal KA, Cooke RG, McArdle D, McClenachan L, Newman MJH, Paredes G, Warner RR, Jackson JBC (2003) Global trajectories of the long-term decline of coral reef ecosystems. *Science* **301**, 955–958. doi:10.1126/science.1085706
- Pastorok RA, Bilyard GR (1985) Effects of sewage pollution on coral-reef communities. *Marine Ecology Progress Series* **21**, 175–189. doi:10.3354/meps021175
- Pisapia C, El Kateb A, Hallock P, Spezzaferri S (2017) Assessing coral reef health in the North Ari Atoll (Maldives) using the FoRAM Index. *Marine Micropaleontology* **133**, 50–57. doi:10.1016/j.marmicro.2017.06.001
- Prazeres M, Martínez-Colón M, Hallock P (2020) Foraminifera as bioindicators of water quality: the FoRAM Index revisited. *Environmental Pollution* **257**, 113612. doi:10.1016/j.envpol.2019.113612
- R Core Team (2021) R: a language and environment for statistical computing. (R Foundation for Statistical Computing: Vienna, Austria.) Available at <https://www.R-project.org/>
- Reymond C, Uthicke S, Pandolfi JM (2012) Tropical foraminifera as indicators of water quality and temperature. In 'Proceedings of the 12th International Coral Reef Symposium'. pp. 9–13. (James Cook University: Townsville, Qld, Australia)
- Ringuet S, Mackenzie FT (2005) Controls on nutrient and phytoplankton dynamics during normal flow and storm runoff conditions, southern Kaneohe Bay, Hawai'i. *Estuaries* **28**, 327–337. doi:10.1007/BF02693916
- Rodgers KS, Jokiel PL, Brown EK, Hau S, Sparks R (2015) Over a decade of change in spatial and temporal dynamics of Hawaiian coral reef communities. *Pacific Science* **69**, 1–13. doi:10.2984/69.1.1
- Sandin SA, Smith JE, DeMartini EE, Dinsdale EA, Donner SD, Friedlander AM, Konotchick T, Malay M, Maragos JE, Obura D, Pantos O, Paulay G, Richie M, Rohwer F, Schroeder RE, Walsh S, Jackson JBC, Knowlton N, Sala E (2008) Baselines and degradation of coral reefs in the Northern Line Islands. *PLoS ONE* **3**, e1548. doi:10.1371/journal.pone.0001548
- Smith SV, Kimmerer WJ, Laws EA, Brock RE, Walsh TW (1981) Kaneohe Bay sewage diversion experiment: perspectives on ecosystem responses to nutritional perturbation. *Pacific Science* **35**, 279–402.
- Uthicke S, Nobes K (2008) Benthic foraminifera as ecological indicators for water quality on the Great Barrier Reef. *Estuarine, Coastal and Shelf Science* **78**, 763–773. doi:10.1016/j.ecss.2008.02.014
- Vehtari A, Gelman A, Gabry J (2017) Practical Bayesian model evaluation using leave-one-out cross-validation and WAIC. *Statistics and Computing* **27**, 1413–1432. doi:10.1007/s11222-016-9696-4
- Vehtari A, Gelman A, Simpson D, Carpenter B, Bürkner P-C (2021) Rank-normalization, folding, and localization: an improved \hat{R} for assessing convergence of MCMC (with discussion). *Bayesian Analysis* **16**, 667–718. doi:10.1214/20-BA1221
- Velásquez J, López-Angarita J, Sánchez JA (2011) Evaluation of the FORAM index in a case of conservation: Benthic foraminifera as indicators of ecosystem resilience in protected and non-protected coral reefs of the Southern Caribbean. *Biodiversity and Conservation* **20**, 3591–3603. doi:10.1007/s10531-011-0152-7
- Wickham H, Averick M, Bryan J, Chang W, McGowan LD, François R, Grolemund G, Hayes A, Henry L, Hester J (2019) Welcome to the Tidyverse. *Journal of Open Source Software* **4**, 1686. doi:10.21105/joss.01686
- Williams ID, Walsh WJ, Schroeder RE, Friedlander AM, Richards BL, Stamoulis KA (2008) Assessing the importance of fishing impacts on Hawaiian coral reef fish assemblages along regional-scale human population gradients. *Environmental Conservation* **35**, 261–272. doi:10.1017/S0376892908004876
- Woodhead AJ, Hicks CC, Norström AV, Williams GJ, Graham NAJ (2019) Coral reef ecosystem services in the Anthropocene. *Functional Ecology* **33**, 1023–1034. doi:10.1111/1365-2435.13331

Data availability. All code and both raw and processed data are available on https://github.com/lrschi94/forams_on_hawaii.

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