Over a Decade of Change in Spatial and Temporal Dynamics of Hawaiian Coral Reef Communities[1]

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Abstract: The Hawai'i Coral Reef Assessment and Monitoring Program (CRAMP) was established in 1999 to describe spatial and temporal variation in Hawaiian coral reef communities in relation to natural and anthropogenic factors. In this study, we analyzed changes over a 14-yr period (1999 to 2012) based on data from 60 permanent reef stations at 30 sites in the main Hawaiian Islands. Overall mean statewide coral cover, richness, and diversity did not vary significantly since the initial surveys, although local variations in coral cover trends were detected. The greatest proportion of stations with significant declines in coral cover was found on the island of Maui (0.4), and Hawai'i Island had the highest proportion of stations with significant increases (0.67). Trends in coral cover at some stations varied over time due to acute (e.g., crown of thorns outbreak) and chronic (e.g., sedimentation) disturbances. Stations with increasing coral cover with the potential for recovery from disturbances were identified for possible management actions in the face of future climate change. The Hawaiian archipelago, located in the center of the subtropical Pacific, has experienced a temporary reprieve from steadily increasing temperatures over the past several decades due to a downturn of temperatures at the end of the last cycle of the Pacific Decadal Oscillation (PDO) in 1998. In 2014, however, temperatures increased dramatically in Hawai'i, resulting in a major coral bleaching event with associated mortality. Temperature models predict severe bleaching events to increase in frequency and intensity in coming decades with concomitant decline in Hawaiian corals. Trends reported in this study provide a baseline that can later be used to test this predicted decline associated with future warming.

The Hawai'i Coral Reef Assessment and Monitoring Program (CRAMP) was established in 1999 to test the hypothesis that reef condition is related to anthropogenic and natural forcing functions and that management practices (various levels of protection) can conserve and restore coral reefs through regulating human impact (Brown et al. 2004). Management needs were addressed to develop a baseline and understand the current status and future stability of Hawaiian reefs (http://cramp.wcc.hawaii.edu). No statewide

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long-term monitoring program existed before the development of CRAMP. Previous monitoring had been fragmentary, addressing local issues with short-term studies by a range of researchers using a variety of methods. Studies conducted at limited spatial and temporal scales can be misleading in the understanding of broad patterns and ecological processes of reefs on a large scale (Hughes and Connell 1999).

CRAMP established a robust baseline for a large number of reefs representing the overall diversity in the state of Hawai'i. Initial results of temporal change after the first 3 yr from 1999 to 2002 were reported by Jokiel et al. (2004). The islands with the highest concentration of human population or highest levels of sedimentation showed the highest declines in coral cover. Coral reef communities experience natural fluctuations over a short duration of several years (Grigg and Dollar 1990). Thus, long-term decadal data are essential to define long-term trends outside natural variation. This report focuses on describing the overall spatial and temporal changes in coral communities spanning the previous 14 yr in the main Hawaiian Islands, with an emphasis on comparisons among islands. We also speculate on potential causes of the observed patterns.

MATERIALS AND METHODS

To provide a diverse representation of coral reefs in the main islands in the state of Hawai'i, site selection criteria included degree of perceived environmental degradation, wave exposure and direction, level of management protection, accessibility, longitudinal range, range of anthropogenic and natural impacts, and level and comparability of pre-existing data. Input on site selection for reefs of interest was also received from nongovernmental organizations, state agencies, and federal agencies involved with the management of nearshore reef areas in Hawai'i.

Thirty-two permanent long-term monitoring sites were selected on hard substrate with two stations at each site. Generally, this design consisted of a shallow station in <5 m of water and a deeper station at depths >5 m (see Table 1).

At each station, 10 randomly selected 10 m transects were permanently marked using stainless steel pins. Thirty of the sites (60 stations) were initially surveyed between 1999 and 2001, with an additional two sites (four stations) added in 2003 and 2004 to fill in spatial gaps and to address concerns about degradation at specific reefs. Detailed methodology is described by Jokiel et al. (2004). The methodology was designed with high statistical power as described by Brown et al. (2004) to distinguish an absolute change of 10% in coral cover annually within a site. This design focused on changes in percentage coral cover within a site because the sites were not randomly selected at the onset.

Initially, digital video and the software program PointCount99 (Dustan, University of Charleston) were used to tabulate substrate type. Advances in digital still photo technology led to improved resolution over video frames, so starting in 2004 nonoverlapping digital images were used to estimate benthic coverage using the software program PhotoGrid (Bird 2001). Before this modification in methodology, an analysis was conducted to ensure that data were comparable between techniques and thus extend the temporal comparison. The variables of interest at each station were percentage coral cover, coral species richness, and coral diversity.

Over the 14-yr survey period, sites were surveyed between two and 14 times (Table 1). Consistent annual sampling was limited by resources or adverse weather conditions. A general linear mixed model (*lmerTest* package) in the R statistical software package (ver. 2.15.3) was used for trend estimation of percentage coral cover by station (R Core Team 2012). Percentage coral cover data were arcsine–square root transformed to meet the assumptions of normality and homogeneity of the variances (Zar 1999). Percentage coral cover was the dependent variable with year (1999–2012) and transect (1–10 for permanent transects at each station, $n = 640$) as random effects. Due to the hierarchical nature of the sampling design, transect was nested in station to focus on transects within each year and across years. A standardized covariate was generated for trend estimation with the year variable starting at year 0 (e.g., Starcevich 2013). The fixed effects or effects of interest in the model were station ($n = 64$) and the year covariate (0–13). Restricted maximum likelihood (REML) in the *lmer* function, which is within the *lmerTest* package, was used to estimate variance due to the unbalanced structure of the data because not all sites were visited annually (Spilke et al. 2005). The Kenward-Rogers (1997) approximation to Satterthwaite's degrees of freedom was used to generate the P value of the t-statistic at $\alpha = .05$.

Explanatory variables such as wave exposure, human population in the watershed, and precipitation in the watershed were not included in the model because the main focus of the paper was simply to examine statewide trends. In addition, gaps in the data set limited using more complex models that examined statistical differences among islands and depths. Therefore, the results focused on simply tabulating the number of sites among islands and depths that experienced significant changes in coral cover. Regression slope estimates were used from the general linear mixed model for the comparison.

Coral species richness and diversity were examined using paired t-tests (MINITAB 14) to explore the variation in coral species composition. Two sites were removed from the results due to abbreviated sampling. Hakioawa, Kahoʻolawe (1999–2002), has not been resurveyed since 2002, and Māhinahina, Maui (2004–2012), was not initiated until 2004.

RESULTS

The average coral cover on transects statewide in 2012 (24.1%, SE ± 0.89) was not significantly different ($t = -0.026$, df = 61, $P = .979$) from the average of coral cover on the same transects when first surveyed between 1999 and 2000 (24.3%, SE ± 0.93) (Figure 1). Although average coral cover did not change significantly statewide, 29 stations showed a decline in coral cover, of which 14 were statistically significant (Table 1, Figure 1).

Maui had the highest proportion of stations (8 out of 18 stations: 0.44) with a significant decline in coral cover, whereas the island of Hawaiʻi had the highest proportion of stations with a significant increase (8 out of 12 stations: 0.67). Regression slope estimates from each station (Table 1) support this pattern and indicated that coral cover on Maui experienced the highest number of sites with significant decreases. Three of 12 stations (0.25) on Oʻahu showed a significant increase in coral cover with an equal number of stations that had a significant decrease in coral cover (Figure 1). On the island of Kauaʻi, two of the 10 stations (0.20) experienced a significant decline in coral cover, one showed a significant increase, and the seven remaining stations (0.70) appeared relatively stable. The largest decline in percentage coral cover was found at the Papaʻula, Maui, 10 m station, which declined from >50% to <5% over 14 yr, and the Kamiloloa, Molokaʻi, 10 m station showed the greatest percentage increase, from <1% to >10% from 2000 to 2012.

Statewide, shallow stations experienced more significant changes in coral cover over the study period (22 of 33 stations with significant changes: 0.67) than deeper stations (7 of 27 stations: 0.26). Significant increases in coral cover were documented at 10 shallow stations (0.30) compared to 12 stations (0.36) with significant decreases. At deeper sites, four stations (0.13) had significant increases and three stations had significant decreases in coral cover. Hawaiʻi Island had the highest proportion of shallow stations (five of six stations: 0.83) that experienced a significant increase in coral cover. Maui had the largest proportion of shallow stations (6 of 11 stations: 0.55) with a significant decline. The deeper stations on Hawaiʻi and Molokaʻi had the highest proportion (0.33) of stations with significant increases compared with the other islands. In contrast, the largest proportion of deep stations with a significant decline in coral cover was on the island of Maui (three of seven stations: 0.43).

Coral species diversity (Shannon-Weiner) did not vary significantly across the state from 1999/2000 to 2012 ($P = .23$). Coral richness within stations exhibited a significant decrease

TABLE 1

CRAMP Sites Showing Depth, Legal Status, Number of Years Surveyed, Coral Cover Regression Slope over the Years Surveyed (Negative Slope Indicates Decline), and *P* Values

Island	Site	Depth (m)	Legal Status[a]	No. Years Surveyed	Slope[b]	*P*[c]
Kaua'i	Hanalei	3	O	10	–1.27	**<0.001**
	Hanalei	8	O	10	–0.41	0.292
	Ho'ai	3	O	4	0.69	**0.011**
	Ho'ai	10	O	4	0.24	0.222
	Limahuli	1	O	5	–0.69	**0.001**
	Limahuli	10	O	7	0.16	0.385
	Miloli'i	3	O	3	0.07	0.660
	Miloli'i	10	O	4	0.13	0.592
	Nu'alolo	3	O	4	–0.05	0.653
	Nu'alolo	10	O	4	–0.49	0.094
O'ahu	Ala Wai	3	O	2	0.18	0.349
	Ala Wai	10	O	2	–0.15	0.978
	Hanauma	3	NT	5	–1.27	**<0.001**
	Hanauma	10	NT	5	0.31	0.589
	He'eia	2	O	6	3.97	**<0.001**
	He'eia	8	O	6	0.16	0.515
	Ka'alaea	2	O	7	–0.83	**0.014**
	Ka'alaea	8	O	6	0.72	**<0.001**
	Kahe Point	3	O	5	–0.14	0.552
	Moku o Lo'e	2	NT	8	2.58	**<0.001**
	Moku o Lo'e	9	NT	8	0.40	0.083
	Pili o Kahe	3	O	5	–0.33	0.051
	Pūpūkea	4	PP	4	0.26	0.258
	Pūpūkea	8	PP	4	0.21	0.491
Moloka'i	Kamalō	3	O	8	–0.83	**0.020**
	Kamalō	10	O	8	–0.56	0.112
	Kamiloloa	3	O	8	–0.19	0.079
	Kamiloloa	10	O	7	0.69	**<0.001**
	Pālā'au	3	O	8	0.28	0.373
	Pālā'au	10	O	8	–0.55	0.080
Kaho'olawe	Hakioawa	3	PP	4	0.24	0.541
	Hakioawa	10	PP	4	–1.17	0.524
Maui	Honolua North	3	NT	14	–0.48	**0.035**
	Honolua South	3	NT	14	–1.64	**<0.001**
	Kanahena Bay	1	NT	12	0.45	0.086
	Kanahena Bay	3	NT	12	1.06	**0.001**
	Kahekili	3	O	13	0.90	**0.006**
	Kahekili	7	O	12	0.47	0.114
	Kanahena Point	3	NT	13	–0.37	**0.011**
	Kanahena Point	10	NT	13	–1.79	**<0.001**
	Ma'alaea	3	O	12	–0.84	**<0.001**
	Ma'alaea	6	O	12	–0.56	**<0.001**
	Māhinahina	3	O	6	–0.27	0.807
	Māhinahina	10	O	7	–0.25	0.656
	Molokini	8	NT	13	0.15	0.600
	Molokini	13	NT	13	–0.05	0.721
	Olowalu	3	O	14	–0.37	0.212
	Olowalu	7	O	14	–0.04	0.997
	Papa'ula	4	O	13	–1.08	**<0.001**
	Papa'ula	10	O	13	–4.28	**<0.001**
	Puamana	3	O	12	–0.02	0.990
	Puamana	13	O	14	0.09	0.282

TABLE 1 (continued)

Island	Site	Depth (m)	Legal Status[a]	No. Years Surveyed	Slope[b]	P[c]
Hawai'i	Ka'apuna	4	O	3	0.56	**0.013**
	Ka'apuna	10	O	4	0.47	0.139
	Kawaihae	3	O	3	–0.84	**0.002**
	Kawaihae	10	O	3	–2.10	<**0.001**
	La'aloa	3	O	4	1.73	<**0.001**
	La'aloa	10	O	4	1.83	<**0.001**
	Laupāhoehoe	3	O	3	1.33	<**0.001**
	Laupāhoehoe	10	O	3	0.47	0.055
	Leleiwi	3	O	3	1.28	<**0.001**
	Leleiwi	10	O	3	–0.59	0.082
	Nenue	5	PP	5	1.32	<**0.001**
	Nenue	10	PP	5	1.18	<**0.001**

[a] O, open access; PP, partially protected; NT, no take.
[b] A positive slope indicates increase in coral cover with possible recovery potential.
[c] Bold P values indicate statistically significant trend over the study period.

since the initial surveys (7.4 ± 0.3 SE in 1999/2000 versus 6.7 ± 0.2 SE in 2012 [P = .02]) due to the appearance and disappearance of uncommon species at various stations that represent a very small fraction of the coral cover. The overall number of species recorded from all stations remained stable at 20 species; however species composition varied slightly among the rarer species such as *Leptoseris incrustans* and *Montipora incrassata*. This result may have been an artifact of the random point sampling on the images, which may not have detected the rare species every time.

Coral cover on the statewide permanent transects was dominated by *Porites lobata* (6.9%) followed by *Montipora capitata* (6.1%), *Montipora patula* (5.0%), *Porites compressa* (3.5%), *Pocillopora meandrina* (1.5%), and *Montipora flabellata* (0.7%). Species composition shifted since the original surveys, with four of the main species increasing in cover and two species decreasing. *Montipora patula* experienced the largest percentage increase (+83.3%), followed by *Montipora capitata* (+56.8%), *Porites lobata* (+12.7%), and *Montipora flabellata* (+2.4%), while *Pocillopora meandrina* (–36.1%) and *Porites compressa* (–22.9%) exhibited a decrease in percentage cover. Hawai'i Island showed no temporal decreases of the main coral species over the survey period. Total cover of *Montipora flabellata* declined on Maui, O'ahu, and Kaua'i, while cover of *Porites compressa* exhibited declines on Moloka'i and O'ahu, and cover of *Porites lobata* showed temporal declines on Kaua'i (Table 2). Species with the strongest skeletal strengths, *Montipora flabellata* (1.2% mean percentage cover at shallow stations, 0.3% mean percentage cover at deep stations), *Pocillopora meandrina* (1.9%, 1.1%), and *Porites lobata* (8.2%, 7.2%) had higher mean coral cover in shallower (<5 m) waters compared with deeper waters (>5 m) (Table 2).

DISCUSSION

Compared with the initial CRAMP survey results reported by Jokiel et al. (2004), the number of stations on the island of Maui experiencing a significant decline in coral cover increased from six to eight. In contrast, more stations (seven versus three) on the island of Hawai'i had a significant increase in coral cover (Figure 2). Between 1999 and 2002 there were five stations out of the 12 surveyed (0.42) on the most populated island of O'ahu that showed a significant decrease in coral cover compared with only three stations in the study reported here (0.25). In addition, more stations (three versus one) on O'ahu are

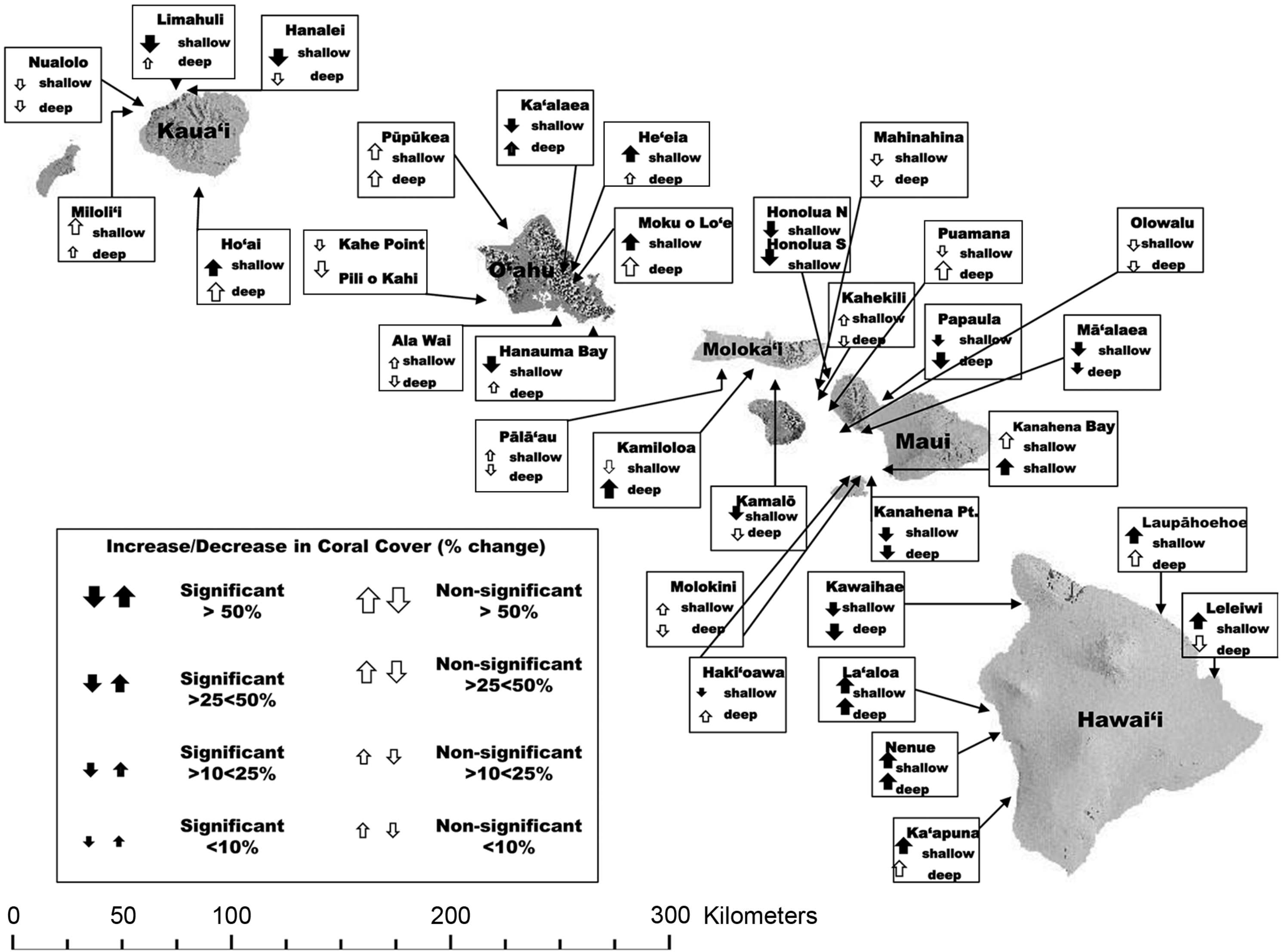

Figure 1. Statewide Coral Reef Assessment and Monitoring stations showing change in coral cover and statistical significance from 1999/2000 to 2012.

TABLE 2

Change in Coral Composition of Main Species by Island (Regression Slope) and Depth (Percentage Cover)

Island/Depth	*Montipora capitata*	*Montipora flabellata*	*Montipora patula*	*Pocillopora meandrina*	*Porites compressa*	*Porites lobata*
Hawai‘i	0.155	0.051	0.063	0.265	0.027	1.460
Maui	0.292	–0.166	0.124	0.017	0.108	0.378
Moloka‘i	0.547	0.034	0.848	0.035	–0.091	0.112
O‘ahu	0.557	–0.010	0.029	0.061	–0.116	0.286
Kaua‘i	0.137	–0.007	0.625	0.029	0.018	–0.025
Kaho‘olawe	0.514	–0.207	0.277	0.169	–0.704	–0.500
Shallow sites (<5 m)	4.13	1.21	1.70	1.89	4.07	8.16
Deep sites (>5 m)	7.06	0.26	6.55	1.13	2.83	7.16

Note: Negative slope indicates a decline; positive slope indicates an increase over all survey years.

currently experiencing a significant increase in coral cover compared with results in the initial paper. Kaua‘i, by comparison, shifted from three stations with a significant increase in coral cover after 2002 to only one station, with the remaining two stations declining in coral cover. Figure 2 summarizes the current trends by island for the stations surveyed. Admittedly, many of the stations were initially selected based on perceived threats and stressors to the reef systems, and therefore the figure may represent a bias toward stations that did not improve or were already in decline.

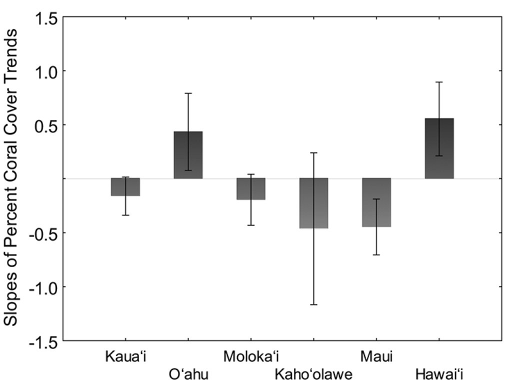

Figure 2. Mean regression slopes of changes in percentage coral cover by island along a longitudinal gradient from west to east. The regression slopes represent changes in percentage coral cover during the study period, with negative slopes indicating a decline in coral cover in contrast to positive slopes that signify an increase in coral cover. Error bars are ±1 SE of the mean. Note that no statistical test was used to evaluate island differences due to gaps in the data set that precluded a more complete analysis at that scale.

Closer examination revealed that trends in percentage coral cover at given stations varied tremendously since the initial CRAMP survey for a variety of potential reasons. Only six of the 60 reported trends in table 1 of Jokiel et al. (2004) held over the full time period of the study. This number more than doubled to 13 when including stations that experienced nonsignificant trends in the earlier study that later were significant with a similar trajectory. The low concordance between surveys at 3 yr and at 13 yr shows the importance of long-term data records to clarify trends above the background noise and reveal potential roles of acute and chronic disturbances that can significantly alter the trend during an intervening period.

Most Hawai‘i reefs are located on island slopes near deep oceanic waters with high wave energy that flushes sediment and pollutants from the system while moderating temperature. Also, Hawai‘i is relatively free of industrial development, mining, and other highly polluting activities, although sediment impact resulting from improper land use practices and feral ungulates is a major problem (Hawai‘i Department of Business, Economic Development, and Tourism 2006). Although over half of all reefs in the wider Pacific region are currently listed as threatened by the World Resources Institute, Hawai‘i has one of the lowest overall threat ratings (Burke et al. 2011).

Thus, overall statewide coral cover and diversity have remained relatively stable since the initial CRAMP survey in 1999, whereas coral cover on reefs in the Caribbean declined by 50% due to bleaching events, storms, and a major decline in coral growth (Wilkinson 2004). Nevertheless, Hawai'i and other areas of the Pacific with relatively healthy coral reefs are now at a threshold of severe and frequent bleaching events projected for the near future (Donner 2009, Hoeke et al. 2011). The Intergovernmental Panel on Climate Change (2013) stated that within the next few decades the thermal limits of corals will be surpassed in most geographic regions, with the highest impact in the Caribbean and the lowest in the central Pacific (Intergovernmental Panel on Climate Change 2013, Hoegh-Guldberg and Bruno 2010).

Acute disturbances such as storm events (Hanalei, Kaua'i, 2003) or crown of thorns outbreaks (Kanahena Point, Maui, 2005) can be seasonal or of a temporary nature (Keough and Quinn 1991). CRAMP stations that showed an acute decline from natural impacts often showed a steady increase in coral cover following the disturbance (Figure 3*a*). In contrast, stations with chronic, recurrent pressure showed inhibited recovery of coral cover (e.g., Mā'alaea and Honolua Bay, Maui) (Figure 3*b*). Several stations on each of the main islands exhibited specific disturbance (e.g., crown of thorns outbreak, sedimentation, nutrification) followed by recovery. Many of those disturbance/recovery events were also documented by other studies that helped explain the declines in coral cover at those stations.

Many stations on the island of Hawai'i experienced an overall increase in coral cover during the study period as indicated by the positive regression slopes in percentage coral cover (Figure 2). The exceptions were the two stations at Kawaihae along the northern section of the West Hawai'i coastline (Figure 1). These results are in agreement with data from the Division of Aquatic Resources West Hawai'i Aquarium Project that has developed extensive spatial and temporal data coverage at 24 sites along the West Hawai'i coastline. West Hawai'i Aquarium Project results showed a significant decline in coral cover since 2003 at six of their seven northern sites that encompass the West Hawai'i coastline (Walsh et al. 2009). In addition, the Division of Aquatic Resources and The Nature Conservancy found drastic declines in reef fishes and associated coral habitat when reviewing historical and recent data at sites near Kawaihae, West Hawai'i (Minton et al. 2012). Minton et al. (2012) found that contributing factors included a decrease in vegetation cover in the adjacent watersheds due to a reduction in rainfall over the preceding 9 yr that increased

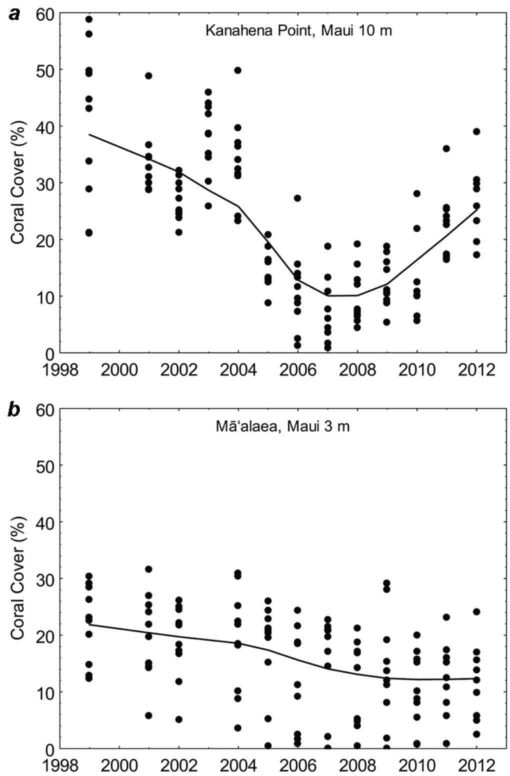

FIGURE 3. *a*, Scatterplot of percentage coral cover from 1999 to 2012 at the Kanahena Point 10 m station on Maui showing the acute impact of the crown of thorns outbreak in 2005; *b*, scatterplot of percentage coral cover from 1999 to 2012 at the Mā'alaea 3 m station on Maui showing the steady decline in cover over the same time period. The solid trend line in both plots represents a Lowess function fitted to the data.

sediment deposition on nearshore reefs. Survey plots in the Pelekane Bay Watershed above the Kawaihae site also showed a decline in vegetation as drought conditions progressed (The Kohala Center 2011). Major sedimentation events occurred during periods of high rainfall (U.S. Geological Survey 2006, 2011).

A predominant pattern of continued decline in coral cover is clearly evident at open access stations on Maui (Table 1, Figure 1). This has been linked to land-based nutrients (Smith et al. 2005, Smith and Smith 2006, Dailer et al. 2010) and low herbivore populations (Walsh et al. 2009). At sites with low grazing, mainly due to heavy fishing pressure that has removed the herbivores, algae compete with coral for available substrate. Walsh et al. (2009) found a relationship between areas with depleted grazers and abundant *Acanthophora spicifera*, a preferred herbivore food (e.g., Māʻalaea), and those with little or no *A. spicifera* and abundant grazers (e.g., Honolua Bay). This led to recent management action of the Kahekili Herbivore Fisheries Management Area where removal of herbivorous fishes is prohibited. At Papaʻula, much of the decline in coral cover has occurred since 2009, when a dramatic increase in the invasive *A. spicifera* was documented (Walsh et al. 2009). In addition to excessive algal growth, other nonindigenous and invasive species may be contributors to the observed declines. Coles et al. (2006) found that enclosed harbors (e.g., Māʻalaea) and disturbed embayments (e.g., Honolua Bay) generally had higher levels of introduced species than open-ocean reefs. This pattern has also been observed in other parts of the Pacific such as Guam (Pauley et al. 2002) and American Samoa (Coles et al. 2003).

Steady decline at sites with open access on Maui are correlated with chronic, localized anthropogenic impacts while marine protected areas (MPAs) and deeper sites farther from land-derived materials have remained stable or experienced slower declines in coral cover. Selig and Bruno (2010) compared coral cover within 310 MPAs worldwide with unprotected reefs and found that MPAs are not only beneficial to restoration of fish populations but also to corals by indirectly reducing fishing pressure, which has been linked to coral degradation and mortality (Wilson et al. 2008).

Honolua Bay, a no-take Marine Life Conservation District, is a notable example. Coral cover data from the two stations going back to 1974 documented a period of stability and then a gradual decline beginning in the mid-1990s (Friedlander et al. 2008). It was hypothesized that agricultural practices in the watershed coupled with low coral recruitment levels contributed to the chronic decline in the coral community (Brown 2004). A dramatic decline in coral cover at the MPA at Kanahena Point (Figure 3*a*) was directly attributed to a crown of thorns (*Acanthaster planci*) outbreak (one per 10 m^2) in 2005 (Walsh et al. 2009). The initial impact reduced coral cover at both the shallow (from 11.8 to 1.1%) and deep (33.9, 14.5%) stations, but there has been a gradual recovery at both stations (shallow: 1.1, 4.5%; deep: 14.5, 26.3%) over the last 7 yr. This localized predation event has also resulted in changes in coral community composition, with a shift from montiporid toward poritid corals. Increases in coral diversity within a reef system such as at this site can increase resistance to future stressors and improve resilience (Birkeland and Lucas 1990, Carpenter 1997).

The reefs along the south shore of Molokaʻi appear to have been primarily influenced by terrestrial sediment input and nearshore sediment transport over the past few decades (Field et al. 2008). In response, the Molokaʻi stations from Kamalō to Kamiloloa (east to west) near the harbor (Figure 1) continued to decline due to historical land-derived sedimentation caused by improper land management and overgrazing by feral ungulates (Roberts and Field 2008). The stations at Kamalō in particular have experienced a slow, steady decline in coral cover. In addition to land-derived sediment impacting the Kamalō stations, two proposed marina developments in the 1970s excavated considerable sediment upcurrent of these monitoring stations (Roberts and Field 2008). The deeper Kamiloloa site, however, increased in coral cover from 0.9% to 10.0% from 2000 to

2012. This deeper site had the highest level of coral settlement among the Moloka'i stations (Brown et al. 2008) and may be far enough removed from sources of sedimentation that it is showing signs of recovery from a previous disturbance (e.g., Hurricane 'Iniki in 1992). The two Pālā'au stations have remained relatively stable since 2000, in part due to the stabilizing influence of the invasive mangroves that have inhibited sediment transport onto the reef (D'Iorio 2008).

The overall pattern of decline on the island of O'ahu reported in Jokiel et al. (2004) has stabilized due to increases in coral cover at sites in Kāne'ohe Bay as well as in the marine protected sites at Pūpūkea (Figure 1). Following historical insults of sewage discharge from 1951 through 1978, increases in coral cover have been documented in Kāne'ohe Bay near CRAMP sites between 1997 and 2011 (J. Stimson, pers, comm.). An extensive rain event in 2006 resulted in a reduction in irradiance, and the associated high levels of nutrients caused a dramatic decline in the macroalga *Dictyosphaeria cavernosa* (Stimson and Conklin 2008). This decline reduced algal dominance and competition for space, allowing reestablishment of formerly displaced coral. The one exception in Kāne'ohe Bay was the shallow Ka'alaea station, which showed a significant decline, attributed to slumping of the upper reef slope. Coral cover was relatively stable at stations located in the Marine Life Conservation District (MLCD) at Pūpūkea and Hanauma Bay. The notable exception was the shallow station at Hanauma Bay, which declined significantly in coral cover over the study period, and most of the decrease appeared to occur after 2002. This wave-sheltered MLCD on the south shore receives over 1 million visitors a year and has more fragile corals based on the coral assemblage than at the Pūpūkea MLCD on O'ahu's north-facing shore. Therefore, it is possible that the shallow station was more prone to damage from physical contact (e.g., Rodgers et al. 2003) and changes in the nearshore water quality from high human use than the deeper station.

Coral zonation patterns reflect coral morphology, skeletal strength, and wave regimes. Species with stronger skeletons such as *Pocillopora meandrina* and *Porites lobata* and encrusting species with low relief such as *Montipora flabellata* showed higher coral cover in shallow waters where wave energy is highest. This pattern of distribution has likely evolved as an adaptive response to disturbance by waves (Rodgers et al. 2003, Storlazzi et al. 2005). Dollar (1982) demonstrated depth stratification of corals in Hawai'i due to wave stress. Corals exhibiting highly branched morphologies, low skeletal strength, and high fracture rates are found in regions with little wave exposure such as embayments and sheltered areas, and lobate and encrusting forms tend to inhabit regions with higher wave energy.

This study focused on station-specific trends since CRAMP was started in 1999. Identifying stations that are improving or stable despite perceived natural and anthropogenic variations will be crucial to direct management strategies in the face of future climate change. The main Hawaiian Islands occupy a unique geographic position in an area of the north-central Pacific that has escaped major bleaching events (Burke et al. 2011) as well as rapid sea level rise (Leuliette 2012) over the past decade. The long-term trend of increasing water temperature in Hawaiian waters, however, indicates that Hawai'i may not be buffered indefinitely from these climatic events. The Hawaiian archipelago experienced a temporary reprieve from steadily increasing temperatures over the past several decades due to a downturn of temperature at the end of the last cycle of the Pacific Decadal Oscillation (PDO) in 1998. We now appear to be moving into another warm phase as evidenced by a major coral bleaching event with associated mortality occurring in Hawai'i during 2014 (Neilson 2014). Temperature models predict severe bleaching events to increase in frequency and intensity in coming decades with concomitant decline in Hawaiian corals (Donner 2009). Trends reported in this study provide a baseline that can later be used to test this predicted decline associated with future warming. In addition, projected changes in the ocean chemistry due to ocean acidification will have profound effects on reef areas globally and in Hawai'i unless carbon emissions are reduced substantially (Hoegh-Guldberg et al. 2007). Consequently, it is imperative that reefs be identified that appear to be more resistant and/or resilient to these perturbations.

The 1999–2000 CRAMP baseline established reliable reference points to evaluate coral cover statewide over time. In addition, comparative studies at the onset (e.g., Brown 2004, Brown et al. 2004) enabled the program to examine earlier temporal data sets at a larger spatial scale than had been previously attempted. The study reported here documented the trends at individual stations and found similar levels of improving and declining reefs, suggesting that overall statewide coral cover and diversity has remained relatively stable since the initial CRAMP survey. The key strategy will be focusing management efforts on the stations that have been declining in a chronic fashion. Even though many of these reefs may have already been in a degraded state when CRAMP was initiated, the current (2012) results will set a new baseline for assessing future declines and potential recovery at reefs targeted for management actions.

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Literature Cited

Bird, C. E. 2001. PhotoGrid: Ecological analysis of digital photographs (downloadable online software). University of Hawai‘i, Honolulu. http://www.photogrid.netfirm.com/.

Birkeland, C., and J. S. Lucas. 1990. *Acanthaster planci:* Major management problem on coral reefs. CRC Press, Boca Raton, Florida.

Brown, E. K. 2004. Reef coral populations: Spatial and temporal differences observed on six reefs off West Maui. Ph.D. diss., University of Hawai‘i at Mānoa, Honolulu.

Brown, E. K., P. L. Jokiel, K. S. Rodgers, W. R. Smith, and L. M. Roberts. 2008. The status of the reefs along South Moloka‘i: Five years of monitoring. Pages 51–58 *in* M. E. Field, S. A. Cochran, J. B. Logan, and C. D. Storlazzi, eds. The coral reef of South Moloka‘i, Hawai‘i: Portrait of a sediment-threatened fringing reef. U.S. Geological Survey Scientific Investigations Report 2007-5101.

Brown, E., E. Cox, P. Jokiel, K. Rodgers, W. Smith, B. Tissot, S. L. Coles, and J. Hultquist. 2004. Development of benthic sampling methods for the Coral Reef Assessment and Monitoring Program (CRAMP) in Hawai‘i. Pac. Sci. 58:145–158.

Burke, L., K. Reytar, M. Spalding, and A. Perry. 2011. Reefs at risk revisited. World Resources Institute, Washington, D.C.

Carpenter, R. C. 1997. Invertebrate predators and grazers. Pages 198–229 *in* C. Birkeland, ed. Life and death of coral reefs. Chapman and Hall, New York.

Coles, S. L., F. L. M. Kandel, P. A. Reath, K. Longenecker, and L. G. Eldredge. 2006. Rapid assessment of nonindigenous marine species on coral reefs in the main Hawaiian Islands. Pac. Sci. 60:483–507.

Coles, S. L., P. A. Reath, P. A. Skelton, V. Bonito, R. C. DeFelice, and L. Basch. 2003. Introduced marine species in Pago Pago Harbor, Fagatele Bay and the National Park Coast, American Samoa. Bishop Mus. Tech. Rep. 26. http://www.bishopmuseum.org/research/pbs/pdf/pagopago.pdf.

CRAMP. Coral Reef Assessment and Monitoring Program, Hawai‘i. http://www.cramp.wcc.hawaii.edu.

Dailer, M. L., R. S. Knox, J. E. Smith, M. Napier, and C. M. Smith. 2010. Using δ^{15}N values in algal tissue to map locations and potential sources of anthropogenic nutrient inputs on the island of Maui, Hawai‘i, USA. Mar. Pollut. Bull. 60:655–671.

D’Iorio, M. 2008. Invasive mangroves and coastal change on Moloka‘i. Pages 129–134 *in* M. E. Field, S. A. Cochran, J. B. Logan, and C. D. Storlazzi, eds. The coral reef of South Moloka'i, Hawai'i: Portrait of a sediment-threatened fringing reef. U.S. Geological Survey Scientific Investigations Report 2007-5101.

Dollar, S. J. 1982. Wave stress and coral community structure in Hawaii. Coral Reefs 1:71–81.

Donner, S. D. 2009. Coping with commitment: Projected thermal stress on coral reefs under different future scenarios. PLoS ONE 4 (6): e5712. doi:10.1371/journal.pone.0005712.

Field, M. E., R. S. Calhoun, C. D. Storlazzi, J. B. Logan, and S. A. Cochran. 2008. Sediment on the Moloka'i reef. Pages 137–144 *in* M. E. Field, S. A. Cochran, J. B. Logan, and C. D. Storlazzi, eds. The coral reef of South Moloka'i, Hawai'i: Portrait of a sediment-threatened fringing reef. U.S. Geological Survey Scientific Investigations Report 2007-5101.

Friedlander, A., G. Aeby, R. Brainard, E. Brown, K. Chaston, A. Clark, P. McGowan, T. Montgomery, W. Walsh, I. Williams, and W. Wiltse. 2008. The state of coral reef ecosystems of the main Hawaiian Islands. Pages 219–261 *in* J. Waddell, ed. The state of coral reef ecosystems of the United States and Pacific Freely Associated States: NOAA Tech. Memo. NOS NCCOS 11.

Grigg, R. W., and S. J. Dollar. 1990. Natural and anthropogenic disturbance on coral reefs. Pages 439–452 *in* Z. Dubinsky, ed. Ecosystems of the world. 25. Coral reefs. Elsevier, Amsterdam.

Hawai'i Department of Business, Economic Development, and Tourism. 2006. Planning for sustainable tourism, project summary report. Document G155.H3. H32.2005. Honolulu. Available from http://dbedt.hawaii.gov/.

Hoegh-Guldberg, O., and J. F. Bruno. 2010. The impact of climate change on the world's marine ecosystems. Science (Washington, D.C.) 328:1523–1528.

Hoegh-Guldberg, O., P. J. Mumby, A. J. Hooten, R. S. Steneck, P. Greenfield, E. Gomez, C. D. Harvell, P. F. Sale, A. J. Edwards, K. Caldeira, et al. 2007. Coral reefs under rapid climate change and ocean acidification. Science (Washington, D.C.) 318:1737–1742.

Hoeke, R. K., P. L. Jokiel, R. W. Buddemeier, and R. E. Brainard. 2011. Projected changes to growth and mortality of Hawaiian corals over the next 100 years. PLoS ONE 6 (3): e18038. doi:10.1371/journal.pone.0018038.

Hughes, T. P., and J. H. Connell. 1999. Multiple stressors on coral reefs: A long-term perspective. Limnol. Oceanogr. 44 (3): 932–940. doi:10.4319/lo.1999.44.3part2.0932.

Intergovernmental Panel on Climate Change. 2013. Climate Change 2013: The Physical Science Basis. IPCC fifth assessment report of the intergovernmental panel on climate change. T. F. Stocker, D. Qin, G.-K. Plattner, M. Tignor, S. K. Allen, J. Boschung, A. Nauels, Y. Xia, V. Bex, and P. M. Midgley, eds. Cambridge: Cambridge University Press.

Jokiel, P. L., E. K. Brown, A. Friedlander, K. S. Rodgers, and W. R. Smith. 2004. Hawai'i Coral Reef Assessment and Monitoring Program: Spatial patterns and temporal dynamics in reef coral communities. Pac. Sci. 58:159–174.

Kenward, M. G., and J. H. Rogers. 1997. Small sample inference for fixed effects from restricted maximum likelihood. Biometrics 53:983–997.

Keough, M. J., and G. P. Quinn. 1991. Causality and the choice of measurements for detecting human impacts in marine environments. Aust. J. Mar. Freshwater Res. 42:539–554.

Leuliette, E. W. 2012. Sea level trend map. National Oceanic and Atmospheric Administration, Laboratory for Satellite Altimetry sea-level rise products, online data, accessed at http://ibis.grdl.noaa.gov/SAT/SeaLevelRise/.

Minton, D., E. Conklin, P. Weiant, and C. Wiggins. 2012. 40 years of decline on Puakō's coral reefs: A review of historical and current data (1970–2010), p. 43. The Nature Conservancy.

Neilson, Brian. 2014. Coral bleaching rapid response surveys September–October

2014. Available from http://dlnr.hawaii.gov/reefresponse/files/2014/10/DARCoral-BleachingSrvy_Results_10.28.2014.pdf.

Paulay, G., L. Kirkendale, G. Lambert, and C. Meyer. 2002. Anthropogenic biotic interchange in a coral reef ecosystem: A case study from Guam. Pac. Sci. 56:403–422.

R Core Team. 2012. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0. http://www.R-project.org.

Roberts, L., and M. E. Field. 2008. Ridge-to-reef: Sediment shed to the island: People, land, and the reefs of South Moloka'i. Pages 133–128 *in* M. E. Field, S. A. Cochran, J. B. Logan, and C. D. Storlazzi, eds. The coral reef of South Moloka'i, Hawai'i: Portrait of a sediment-threatened fringing reef. U.S. Geological Survey Scientific Investigations Report 2007-5101.

Rodgers, K. S., C. Newtson, and E. F. Cox. 2003. Mechanical fracturing of dominant Hawaiian corals in relation to trampling. J. Environ. Manage. 31:377–384.

Selig, E. R., and J. F. Bruno. 2010. A global analysis of the effectiveness of marine protected areas in preventing coral loss. PLoS ONE 5 (2): 1–7.

Smith, C. E., and J. E. Smith. 2006. Algal blooms in North Kīhei: An assessment of patterns and processes relating nutrient dynamics to algal abundance. Report to City and County of Maui.

Smith, J. E., J. W. Runcie, and C. M. Smith. 2005. Characterization of a large-scale ephemeral bloom of the green alga *Cladophora sericea* on the coral reefs of West Maui, Hawai'i. Mar. Ecol. Prog. Ser. 302:77–91.

Spilke, J., H. P. Piepho, and X. Hu. 2005. Analysis of unbalanced data by mixed linear models using the MIXED procedure of the SAS system. J. Agron. Crop Sci. 191:47–54.

Starcevich, L. A. H. 2013. Trend and power analysis for National Park Service marine data from 2006 to 2010: Pacific Island Network. Natural Resource Technical Report NPS/PACN/NRTR 2013/771. National Park Service, Fort Collins, Colorado.

Stimson, J., and E. Conklin. 2008. Potential reversal of a phase shift: The rapid decrease in the cover of the invasive green macroalga *Dictyosphaeria cavernosa* Forsskål on coral reefs in Kaneohe Bay, Oahu, Hawaii. Coral Reefs 27:717–726.

Storlazzi, C. D., M. E. Field, P. L. Jokiel, S. K. Rodgers, E. Brown, and J. D. Dykes. 2005. A model for wave control on coral breakage and species distribution, southern Molokai, Hawaii. Coral Reefs 24:43–55.

The Kohala Center. 2011. Pelekane Bay Watershed Resoration Project. Aug. 2009–Feb. 2011, p. 57. Technical Report. Waimea, Hawai'i.

U.S. Geological Survey. 2006. Geologic resource evaluation of Pu'ukoholā Heiau National Historic Site, Hawai'i. Part II: Benthic habitat mapping. Scientific Investigations Report 2006-5254.

———. 2011. Coastal circulation and sediment dynamics in Pelekane and Kawaihae Bays, Hawaii. Geological Survey Open-File Report 2012.

Walsh, W., R. Sparks, C. Barnett, C. Couch, S. Cotton, D. White, K. Stone, and E. Conklin. 2009. Long-term monitoring of coral reefs of the Main Hawaiian Islands. Final Report, NOAA Coral Reef Conservation Program, State of Hawai'i Monitoring Report NA06NOS4260113.

Wilkinson, C. 2004. Status of coral reefs of the world: 2001. Vol. 1. Global Coral Reef Monitoring Network, Australian Institute of Marine Science, Townsville.

Wilson, S. K., R. Fisher, M. S. Pratchett, N. A. Graham, N. K. Dulvy, R. A. Turner, A. Cakacaka, N. V. C. Polunin, and S. P. Ruston. 2008. Exploitation and habitat degradation as agents of change within coral reef fish communities. Glob. Change Biol. 14:2796–2809.

Zar, J. 1999. Biostatistical analysis. 4th ed. Prentice-Hall, Upper Saddle River, New Jersey.