

Linking coral reef health with terrestrial anthropogenic disturbance on the west coast of Hawai'i

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ABSTRACT

Coral reefs are declining worldwide. Aggregated anthropogenic disturbance (AAD) from coastal tourism, agriculture, and urban development represent a broad class of potential drivers for this decline. Yet the mechanisms by which AAD causes coral decline remain ambiguous. We surveyed coral reef cover and coral disease rates at eight sites on the west coast of Hawai'i, HI, USA to examine correlations between AAD and coral reef health. AAD was assessed by two contrasting methods: local expert knowledge and GIS analysis of land use. We also took water samples at each site to measure the concentrations of chlorophyll a and total suspended solids. We found trends for higher disease rates in sites that were classified as impacted according to local expert opinion, but these trends did not retain their statistical significance when inter-and intra- site variability were rigorously accounted for using generalized linear mixed effects models. There was no correlation between the expert-based measures of AAD and the GIS variables we examined. We conclude that there is some evidence supporting correlation between AAD and coral reef health, but that general conclusions are difficult to draw because of the natural variability in the data, and because complex patterns in landscape structure preclude simple analyses of their potential impacts on coral health.

INTRODUCTION

Coral reefs are biologically diverse and economically important ecosystems (Moberg & Folke 1999). They provide ecological services essential to humans, such as fisheries, coastal protection from waves, and pharmacological compounds (Moberg & Folke 1999). These same coral reef ecosystems are declining worldwide (Jackson 2001), suffering massive and long-term decreases in abundance and diversity. These declines have been correlated with such factors as water and atmospheric pollution, overfishing, disease, and tourism (Rogers 1990, Hughes 1994, Jackson 1997, Jackson *et al.* 2001, Rodgers & Cox, 2003, Wolanski *et al.* 2003, Hoegh-Guldberg *et al.* 2007, Carpenter *et al.* 2008). Yet, how these processes interact to determine the fate of coral reefs over space and time remains ambiguous. For instance, terrestrial anthropogenic disturbances from tourism, agriculture, and urban development have been hypothesized to have combined detrimental effects on reef health, but because their complex interactions preclude simple experiments, hypotheses relating coral decline to aggregated anthropogenic disturbance (AAD) have not been widely tested (Hoegh-Guldberg *et al.* 2007).

In contrast to our poor understanding of the ultimate effects of AAD, many of the associated proximate drivers of coral decline are better understood. First, anthropogenic nutrient inputs have been associated with increased density of macroalgae that competitively exclude coral (Done & Potts 1992, Huges 1994, Lapointe 1997, Steneck 1997, Williams *et al.* 2008). Second, increased sediment load from agriculture and industrial waste smothers reefs and reduces light available for photosynthesis (Rogers 1990, van Katwijk 1993). Finally, sedimentation and nutrient enrichment are thought to increase disease prevalence (Harvell *et al.* 1999, Lafferty 2004) by speeding the evolution of virulence in reef ecosystems (Ewald 1995) and depressing coral immune function (Harvel *et al.* 1999). Much effort has been devoted to understanding the proximate mechanisms of coral decline, but less attention has been given to how these mechanisms might interact at the landscape scale to determine coral reef health.

The big island of Hawai'i provides an ideal setting to study the impacts of AAD on reef health. This is because the reefs here are composed of relatively few species, and adjacent areas of reef experience differential levels of AAD. The island of Hawai'i is currently experiencing rapid rates of population and economic growth, with lava fields converted to resorts, residential areas, and golf-courses. Since development is relatively new, pockets of

natural coastline are also being preserved, creating a mosaic coastline with a full range of human impacts. Prior work has suggested that coral populations on the island are suffering from anthropogenic impacts, as rapid human development has increased land-base pollution (Hamnett *et al.* 2006, Williams *et al.* 2008). Tourism is another problem for coral reefs on Hawaiian islands, as direct damage from trampling suppresses coral growth (Rodgers & Cox, 2003). Though exact causes have yet to be determined, disease and coral bleaching have also been recorded in Hawaiian corals (Aeby 2007, Rodrigues *et al.* 2008a, b). The combination of relatively low species diversity and combined hazards makes Hawai'i a useful system to be investigated.

In this study we test for correlations between AAD and coral health at eight sites on the west coast of Hawai'i. We use two alternative measures of AAD, one based on local expert opinion, and the other from GIS analysis of landcover data. To assess coral health, we performed surveys at each site of coral cover and disease prevalence.

METHODS

Study Site

Four pristine and four impacted sites were surveyed on the west coast of Hawai'i (Table 1, Fig. 1), with the differences between pristine and impacted sites (hereafter referred to as "treatment" differences) selected by a practitioner from the Kohala Center of Waimea, Hawaii. Pristine sites (Lapakahi, Mauu'mae, Hookena and Manini Beach) were categorized as having low human development and low numbers of tourists. Conversely, impacted sites (Spencer Beach, Pauoa Beach at Fairmont Orchid, Anaehoomalu Bay and Kahalu'u Beach) were situated next to developed areas, such as resorts and golf courses and received a considerable number of visits by tourists throughout the year. Kahalu'u Beach Park, for instance, one of the most popular skin diving beaches on the Big Island, is visited by approximately 350,000 tourists per year (County of Hawai'i 1998). Sites were accessible by land and shallow enough to be surveyed with snorkel equipment only.

Study Species

Porites lobata Dana (1846) and *Pocillopora meandrina* Dana (1846) are the dominant coral species on Hawaiian reef ecosystems, being found in both back and fore reefs (Gosliner *et al.* 1996). *P. lobata* grows to form large lobes and the colony itself can cover several meters. The cauliflower coral, *P. meandrina*, forms compact branching colonies on hard substrate and the dichotomous branches usually extend from the initial growing point.

Sampling Design

At each site, three 10-m transects were randomly placed on areas with the greatest proportion of continuous reef. This prevented macroscale variation in reef coverage from confounding estimates of within quadrat coral cover. All transects were established at snorkeling depth (1-5 m). Four $\frac{1}{2}$ m² quadrats were randomly placed on each side of the transect for a total of 8 quadrats per transect. We measured percent cover of each of the two sampled coral species as well as other reef components (other coral, algae, sediment, bare rock, sand, etc). Note that only *P. lobata* and *P. meandrina* were identified to species level, while all other corals were lumped into one category called “other corals”. For both coral species, the number of individuals was counted and the presence of disease (tumors and/or trematodiasis) was recorded. Tumors are skeletal growth anomalies for which the cause is unknown (Domart-Coulon *et al.* 2006), and trematodiasis is caused by the trematode *Podocotyloides stenometra* and is characterized by pink, swollen nodules (Aeby 2007). Disease prevalence was then calculated as the proportion of diseased individuals.

For each transect we collected a 1-liter bottle sample of water to measure total suspended solids (TSS), and chlorophyll *a*. Samples were stored on ice and in the dark until processing, performed within 5 hours of collection. To measure TSS we used a hand pump to filter 500 ml of sampled water through a pre-weighed filter paper. These papers were dried in an oven for 24 hrs at 60 °C then weighed again. TSS was calculated as the difference between the final dry weight and that of the pre-weighed filter paper. To measure chlorophyll *a* we filtered 500 ml of sampled water through a filter paper as for TSS, and then stored these filters in 20 ml 90% ethanol in the dark for 24 hours. We used a fluorometer (Aquafluor™, Turner Designs) to estimate the chlorophyll *a* from the ethanol solution (Maxwell and Johnson 2000).

GIS Analyses

In order to quantify land-based impacts, such as agricultural runoffs and pollution, we recorded the amount of anthropogenic landcover surrounding the sampling sites. Landcover data from the island (USGS 2005) was extracted using Arc View 9.3 (ESRI 2009). For each sampling site the number of ha agricultural cover, urban development, and natural areas was recorded for circular buffers with radii of 0.5, 1, and 5 km respectively. These variables were used as inputs into statistical models to test for correlations with coral cover and disease prevalence. We also assessed whether the GIS analysis distinguished between pristine and impacted sites.

RESULTS

Multiple comparisons using pairwise t-tests ($\alpha=0.05$) revealed few differences in TSS between the sites ($I1=I2=I6=P2=P5=P6 < I3=P1$). Pairwise differences in chlorophyll *a* ($I1=I3 > I2=P1 > I6=P6 > P1=P5$) among the sites were more consistent with the hypothesis of differences in water chemistry between impacted and pristine sites. However, there was significant overlap due to high inter-site variability (Fig. 2).

Aggregating the data by treatment revealed significant differences between the distributions of infection rates in pristine and impacted sites (two-sided Kolmogorov-Smirnov test, $p=0.001$). In particular, high infection rates were observed more often in impacted sites than pristine sites (Fig. 4). Aggregating the data by treatment also revealed significant differences in the distribution of coral cover between pristine and impact sites (Fig. 4). Quadrats with complete coral cover were more likely to be found in pristine than impacted sites (two-sided Kolmogorov-Smirnov test, $p=0.03$). Pooling the data by site, there was a trend for pristine sites to have a higher proportion covered with *P. meandrina* (logistic regression on average coverage in $n=8$ sites, $p=0.189$), but the sites did not differ significantly in the proportion covered with *P. lobata* ($p=0.85$).

To properly account for random within-transect and within-site variation in coral cover and infection rate, we performed logistic regression using generalized linear mixed effects models (GLMMs) with treatment and GIS variables as fixed factors and transect nested within

site as random factors. We fit separate models for treatment and GIS data at each scale, on proportion coral cover and proportion infected, respectively. The GLMMs revealed no significant differences in coral cover between pristine and impacted sites, but a trend toward higher infection rates in impacted sites ($p=0.13$; Table 3). Models for the GIS data were ambiguous: different factors were significant at varying spatial scales and the slopes of the relationships often pointed in opposing directions from one scale to the next. This suggests that the model is over-fitting the data. To address this we sequentially removed terms using a stepwise AIC-based procedure. This revealed that none of the GIS models were better than the null model, suggesting that variation in coral cover and infection rates was strongly influenced by random variation between sites and quadrats, rather than the effects of treatment or landscape structure. Plotting the sites according to the amount of natural and urban areas present within the 3 buffer sizes did not reveal significant clustering of pristine and impacted sites (Fig. 3). Repeating this procedure with agricultural and urban areas pooled did not significantly change the results.

DISCUSSION

Corals are the main component of reef ecosystems, making the entire reef community sensitive to declines in coral health. Although many of the proximate drivers of coral decline are known, the correlations between aggregated anthropogenic disturbance (AAD) and coral health in a landscape-ecosystem context are not well understood. We tested such correlations here using two measures of AAD, one based on expert opinion and the other on GIS data, and two measures of coral health—coral cover and disease prevalence.

Using less rigorous statistical analyses, we observed significant differences in coral cover and tumor frequency between impacted and pristine sites. However, the GIS data revealed no correlations between our measures of terrestrial anthropogenic disturbance and coral health or with expert classification of the sites. Furthermore, in the more rigorous GLMM analysis, which accounted for site- and transect-level variability, coral cover was not significantly correlated within any measure of AAD we considered. We, therefore, cannot generalize AAD-coral health correlations, since the results depended on how we analyzed the data and on what aspects of AAD and coral health were considered.

We suspect that our ability to generalize the results is hindered in part by the large degree of inter- and intra-site variability. Isolating the effects of a specific disturbance on coastal marine systems is inherently difficult given the complexity, high spatial and temporal variability and inability to manipulate treatments as one might do on land (Rodgers and Cox, 2003, Jokieli *et al.*, 2004). Coral reefs are among the most complex ecosystems in the world, shaped by a myriad of biotic and abiotic factors (Sale, 2008). As such, pairing sites by proximity to control for physical factors in this study did not eliminate large site variability. For example, pristine Manini Beach and Hookena sites were situated close together along the coast and both found in protected coves, but coral cover was much lower at Hookena due to a lack of rocky outcrops, a necessary substrate for coral formation. Other important abiotic factors which varied among the sites, for which we did not control, include wave action and direction, freshwater seepage, bottom rugosity, sediment grain size and depth (Jokieli *et al.*, 2004). Total suspended solids and chlorophyll *a* are sensitive to short-term temporal variability given the important effects of precipitation events and development activities. Consequently, water quality variables would be better measured with temporal replication when comparing sites to one another. In contrast, we only measured these variables once per site, so systematic ecological differences between sites may have been difficult to detect.

With so much variability, long term monitoring of permanent plots is needed to measure impacts of human disturbance on coral health. Larger and longer term studies show that Hawaiian reefs are being degraded, but slowly, which may give the impression that the health of near-shore reefs remains relatively good (Jokieli *et al.*, 2004). Jokieli *et al.* (2004) emphasized the need for long term monitoring at a larger number of sites under such circumstances. With larger data sets, degradation of Hawaiian reefs has been observed and correlated with higher human densities (Jokieli *et al.*, 2004); though, they also only showed trends between human disturbance and coral health. Biomonitoring professionals advocate multiple survey techniques to accommodate for the variability among coral reefs (Coyer 1990, Rogers *et al.* 1994). Our decision to use transect sampling was based on maximizing information and efficiency; however, relying on this technique alone may not have been optimal for sites with discontinuous coral. The fact that we observed significant trends with pooled data despite high within and between site variability suggests that long-term studies with more statistical power might reveal significant effects long suspected by expert practitioners.

Expert knowledge and GIS differed greatly and indicate that integration of qualitative and quantitative assessments may best represent land-based disturbance. Expert knowledge benefits from an unconscious integration of many impacts, with a level of sophistication not easily obtained using GIS. However, this type of intuitive categorization is inherently subjective, and difficult to replicate scientifically. On the other hand, while GIS may be objective it may not function at a fine enough resolution to capture small scale impacts that have important consequences for coral health, such as tourism. Development immediately adjacent to the beach may also be hard to quantitatively compare using GIS. Coastal development on Hawaii is relatively recent and rapid; therefore, GIS layers also risk providing out-dated information. GIS has proven to be a powerful tool for landscape level-analyses, but our study highlights a need to incorporate expert knowledge or ground truthing to GIS data.

While we may be able to measure proximate causes to reef deterioration, integrating impacts over the reef community poses a greater challenge. Individually, the negative impacts of humans, such as trampling (Kay & Liddle, 1989; Hawkins & Robers, 1993), increased sedimentation, organic matter, and nitrogen (Jokiel *et al.*, 2004) are unequivocal. However, many disturbances act on the coral community simultaneously and little is known about how they interact. For example, coral stress induced by ocean warming could result in exaggerated impacts of localized disturbances, such as trampling, if the coral cannot regenerate over time. There is a need, therefore, to integrate terrestrial landscape and marine ecosystems over time and space and find methods of confronting the ecological and anthropogenic variability inherent in coral health assessments.

LITERATURE CITED

- Aeby, G.S. (2007) Spatial and temporal patterns of *Porites* trematodiasis on the reefs of Kaneohe Bay, Oahu, Hawaii. *Bulletin of Marine Science*, 80:209-218.
- Belliveau, S.A.; Paul, V.J. (2002) Effects of herbivory and nutrients on the early colonization of crustose coralline and fleshy algae. *Marine Ecology Progress Series*, 232:105-114.
- Carpenter, K.E.; Abrar, M.; Aeby, G., *et al.* (2008) One-third of reef-building corals face elevated extinction risk from climate change and local impacts. *Science*, 321:560-563.

- Coyer J., Witman J. 1990. The Underwater Catalog: A Guide to Methods in Underwater Research. Shoals Marine Laboratory. Cornell University. New York. 72pp.
- The Kohala Center, County of Hawai'i (1998). Impacted beaches survey.
- Domart-Coulon, I.J.; Traylor-Knowles, N.; Peters, E.; Elbert, D.; Downs, C.A.; Price, K.; Stubbs, J.; McLoughlin, S.; Cox, E.; Aeby, G. Brown, P.R.; Ostrander, J.K. (2006). Compressive characterization of skeletal tissue growth anomalies of the finger coral *Porites compressa*. *Coral Reefs*, 25: 531-543.
- Done, T.J; Potts, D.C. (1992) Influences of habitats and natural disturbances on contributions of massive porites corals to reef communities. *Marine Biology*, 114:479-493.
- ESRI (2009) Arc view v.9.3. Richmond, California.
- Ewald, P.W. (1995) The evolution of virulence – a unifying link between parasitology and ecology. *Journal of Parasitology*, 81:659-669.
- Gosliner T.; Behrens, D.; Williams G. (1996) Coral reef animals of the Indo-Pacific: animal life from Africa to Hawaii exclusive of the vertebrates. Monterey, California: Sea Challengers.
- Hamnett, M.; Lui, M.; Johnson, D. (2006) Fishing, ocean recreation, and threats to Hawaii's coral reefs. Social Science Research Institute, University of Hawaii at Manoa, Hawaii: 6 pp.
- Harvell, C.D.; Kim, K.; Burkholder, J.M., *et al.* (1999) Review: Marine ecology - Emerging marine diseases - Climate links and anthropogenic factors. *Science*, 285:1505-1510.
- Hawkins, J.P.; Roberts, C.M. (1993) Effect of recreational scuba diving on coral reefs – trampling on reef-flat communities. *Journal of Applied Ecology*, 30:25-30.
- Hoegh-Guldberg, O.; Mumby, P.J.; Hooten, A.J., *et al.* (2007) Coral reefs under rapid climate change and ocean acidification. *Science*, 318:1737-1742.
- Hughes, T.P. (1994) Catastrophes, phase-shifts, and large-scale degradation of a Caribbean coral-reef. *Science*, 265:1547-1551.
- Hunter, C. L. & Evans C. W. (1995) Coral reefs in Kaneohe Bay, Hawaii: two centuries of western influence and two decades of data. *Bulletin of Marine Science*, 57:501-515.
- Jackson, J.B.C. (2001) What was natural in the coastal oceans? *Proceedings of the National Academy of Sciences of the United States of America*, 98:5411-5418.
- Jackson, J.B.C.; Kirby, M.X.; Berger, W.H., *et al.* (2001) Historical overfishing and the recent collapse of coastal ecosystems. *Science*, 293:629-638.
- Jackson, J.B.C. (1997) Reefs since Columbus. *Coral Reefs*, 16:S23-S32.

- Jokiel, P.L., Brown, E.K., Friedlander, *et al.* (2004) Hawai'i coral reef assessment and monitoring program: spatial patterns and temporal dynamics in reef coral communities. *Pacific Science*, 58:159-174.
- Kay, A.M.; Liddle, M.J. (1989) Impact of human trampling in different zones of a coral-reef flat. *Environmental Management*, 13:509-520.
- Lafferty, K.D.; Porter, J.W.; Ford, S.E. (2004) Are diseases increasing in the ocean? *Annual Review of Ecology Evolution and Systematics*, 35:31-54.
- Lapointe, B.E. (1997) Nutrient thresholds for bottom-up control of macroalgal blooms on coral reefs in Jamaica and southeast Florida. *Limnology and Oceanography*, 42:1119-1131.
- Lessios, H. A. (1988) Mass mortality of *Diadema antillarum* in the Caribbean: What have we learned? *Annual Review of Ecology Evolution and Systematics*, 19:371-393.
- Maxwell, K. and Johnson, G.N. (2000) Chlorophyll fluorescence-a practical guide. *Journal of Experimental Botany* 51:659-668.
- McCook, L.J.; Jompa, J; Diaz-Pulido, G. (2001) Competition between corals and algae on coral reefs: a review of evidence and mechanisms. *Coral Reefs*, 19:400-417.
- Moberg, F.; Folke, C. (1999) Ecological goods and services of coral reef ecosystems. *Ecological Economics*, 29:215-233.
- Orr, J.C.; Fabry, V.J.; Aumont, O., *et al.* (2005) Anthropogenic ocean acidification over the twenty-first century and its impact on calcifying organisms. *Nature*, 437:681-686.
- R Development Core Team (2008). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL <http://www.R-project.org>.
- Rogers, C.S. (1990) Responses of coral reefs and reef organisms to sedimentation. *Marine Ecology-Progress Series*, 62:185-202.
- Rogers, C.S., G. Garrison, R. Grober, Z. Hillis, M. Franke. 1994. Coral Reef Monitoring Manual for the Caribbean and Western Atlantic. National Park Service, Virgin Islands National Park.
- Rodgers, K.S; Cox, E.F. (2003) The effects of trampling on Hawaiian corals along a gradient of human use. *Biological Conservation*, 112:383-389.

- Rodrigues, L.J; Grottoli, A.G; Lesser, M.P. (2008) Long-term changes in the chlorophyll fluorescence of bleached and recovering corals from Hawaii. *Journal of Experimental Biology*, 211:2502-2509.
- Rodrigues, L.J; Grottoli, A.G; Pease, T.K. (2008) Lipid class composition of bleached and recovering *Porites compressa* Dana, 1846 and *Montipora capitata* Dana, 1846 corals from Hawaii. *Journal of Experimental Marine Biology and Ecology*, 358:136-143.
- Sale, P.F. (2008) Management of coral reefs: Where we have gone wrong and what we can do about it. *Marine Pollution Bulletin*, 56:805-809.
- Steneck, R.S. (1997) Crustose corallines, other algal functional groups, herbivores and sediments: complex interactions along reef productivity gradients. *Proc 8th International Coral Reef Symposium*, 1:695–700
- van Katwijk, M.M.,N. E Meier, R. van Loon, E. M. van Hove, W. B. J. T. Giesen, G. van der Velde, C. den Hartog. 1993. Sabaki River sediment load and coral stress: correlation between sediments and condition of the Malindi-Watamu reefs in Kenya (Indian Ocean). *Marine Biology* 117:675-683.
- Williams, I.D.; Walsh, W.J.; Schroeder, R.E., *et al.* (2008) Assessing the importance of fishing impacts on Hawaiian coral reef fish assemblages along regional-scale human population gradients. *Environmental Conservation*, 35:261-272.
- Wolanski, E; Richmond, R; McCook, L, *et al.* (2003) Mud, marine snow and coral reefs - The survival of coral reefs requires integrated watershed-based management activities and marine conservation. *American Scientist*, 91:44-51.

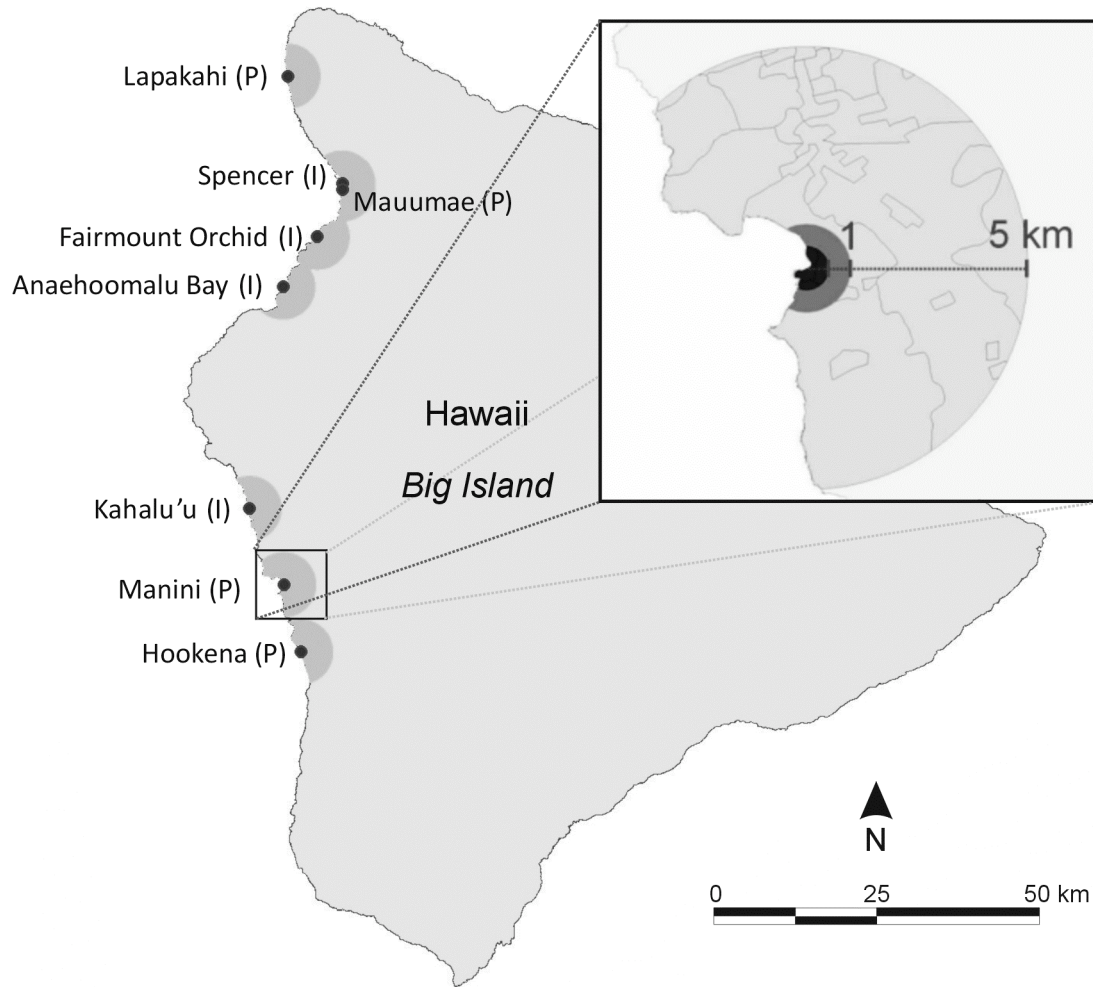


Figure 1. Map of the 8 study sites on the west coast of Hawai'i. Sites were classified with respect to the amount of anthropogenic disturbance using expert knowledge and, separately, based on GIS analysis. At each site we measured two indicators of coral health: percentage cover and infection probability.

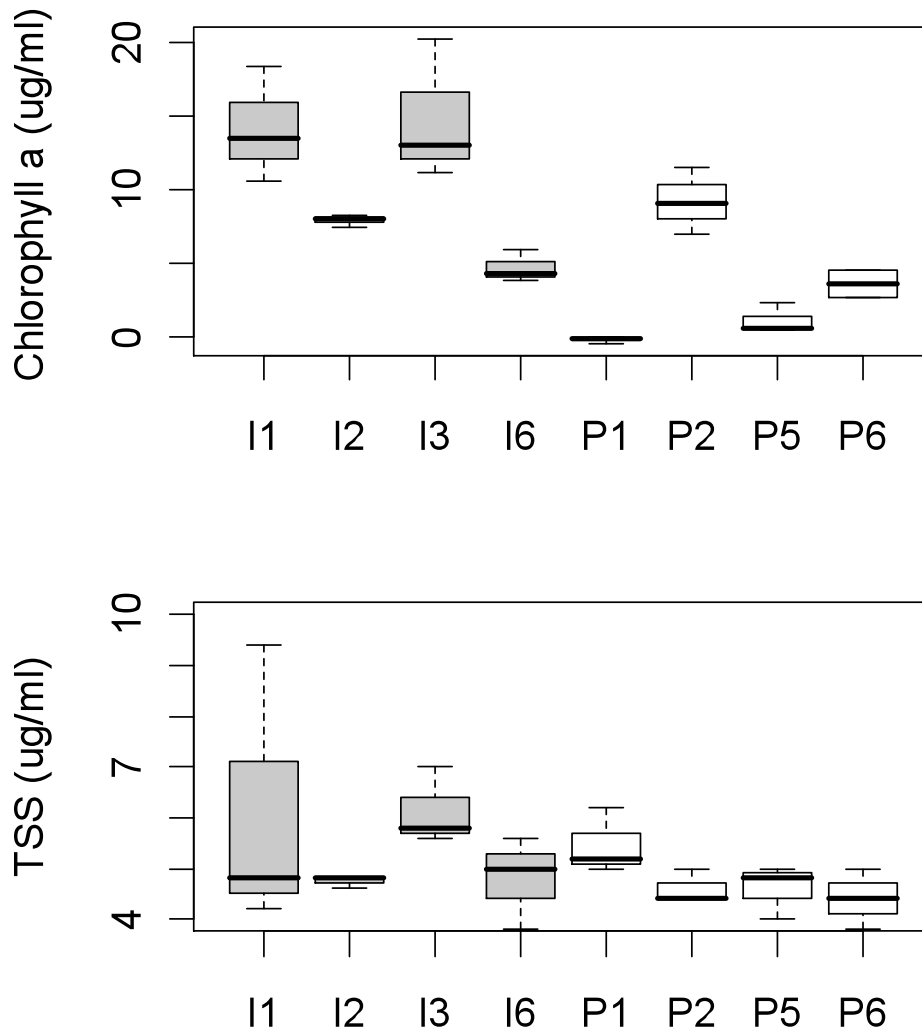


Figure 2: Chlorophyll *a* and total suspended solids (TSS) concentration at each of the 8 sites based on 3 replicate measures at each site. Gray fill stands for impacted sites and empty fill stands for pristine sites.

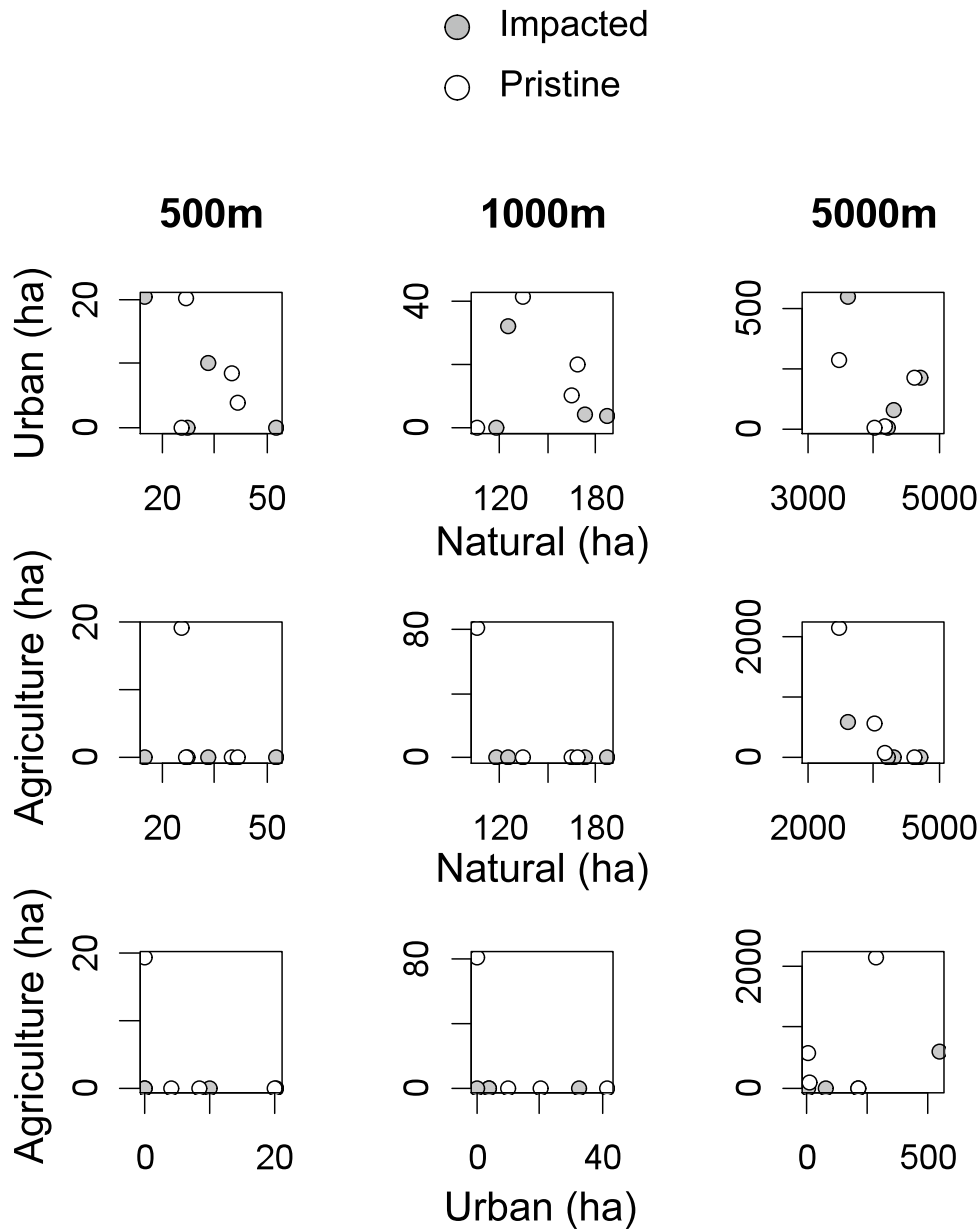


Figure 3: Comparing six near-shore coral reefs in terms of their expert classification as either pristine or impacted, and the number of ha of surrounding natural, urban, and agricultural cover at 3 spatial scales.

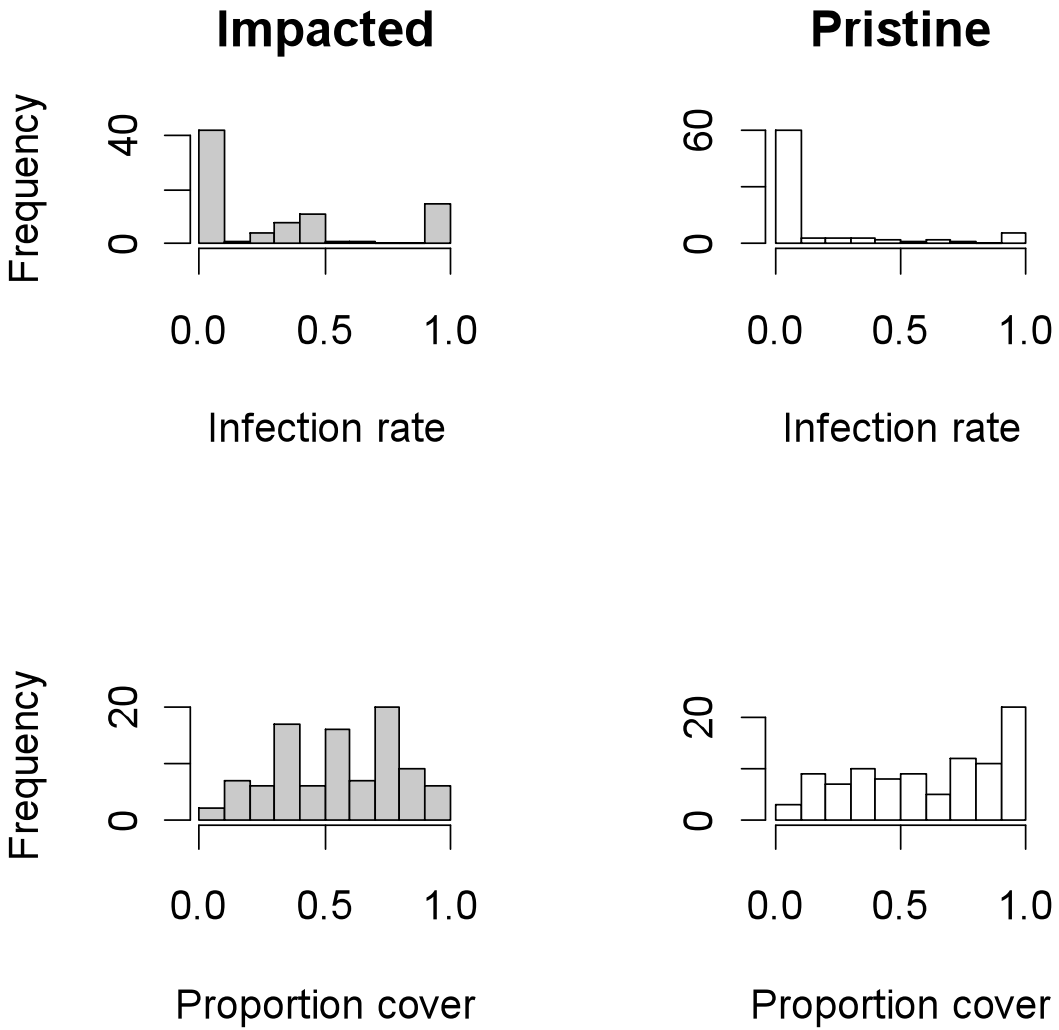


Figure 4: Frequency distributions of infection rates and coral cover the 4 impacted and 4 pristine sites.

Table1: Description of sites with respect to their human impact, average salinity, and depth.

Site name	Impact/ Pristine	Justification	Average Salinity (ppt)	Average Depth (m)
Lapakahi	P	No development	35.3	2.0
Mauu'mae	P	No development, but recent fire	35.7	3.0
Manini Beach	P	Some houses	40.3	3.0
Hookena	P	No development	37.0	2.8
Anaehoomalu Bay	I	Coastal development	34.0	1.5
Spencer Beach	I	County park, sediment input from Kawaihae harbor	34.7	1.0
Pauoa Beach at Fairmont Orchid	I	Sedimentation, resorts, golf course and imported sand	33.3	3.0
Kahalu'u Beach	I	Outrigger hotel has own (minimal) sewage treatment plant. Wastewater released into ocean.	35.7	0.5

Table 2: Results of fitting generalized linear mixed effects models (GLMM) to the coral cover and infection rate data for the 8 sites as a function of expert classification as either pristine or impacted (“treatment”). Table shows coefficient estimates as logit-transformed mean proportions, their standard errors, standardized normal deviates and p values.

I. Coral cover

	Est	SE	z	p
Intercept	0.29	0.50	0.58	0.56
Treatment	0.49	0.70	0.70	0.48

II. Infection rate

	Est	SE	z	p
Intercept	-1.32	0.50	-2.66	0.01
Treatment	-1.12	0.73	-1.54	0.12

Table 3: Results of fitting generalized linear mixed effects models (GLMM) to the coral cover and infection rate data for the 8 sites as a function of 3 GIS variables at 3 different scales. Because GIS variables were correlated, we performed separate analyses on each possible pair at each spatial scale. Table shows coefficient estimates as logit-transformed mean proportions, their standard errors, standardized normal deviates and p values.

I. Coral cover

	500m				1000m				5000m			
	Est.	SE	z	p	Est.	SE	z	p	Est.	SE	z	p
Intercept	0.54	0.30	1.77	0.08	0.53	0.35	1.51	0.13	0.54	0.17	3.10	0.00
Urban	0.61	0.33	1.86	0.06	0.24	0.38	0.64	0.52	0.05	0.19	0.28	0.78
Agriculture	0.25	0.33	0.76	0.44	0.11	0.38	0.29	0.77	0.90	0.20	4.54	0.00
Intercept	0.54	0.31	1.71	0.09	0.54	0.34	1.55	0.12	0.54	0.31	1.75	0.08
Urban	0.56	0.38	1.48	0.14	0.23	0.35	0.67	0.51	0.21	0.34	0.60	0.55
Natural	0.07	0.37	0.19	0.85	0.25	0.35	0.71	0.48	-0.43	0.34	-1.27	0.21
Intercept	0.53	0.35	1.51	0.13	0.53	0.35	1.53	0.12	0.54	0.15	3.68	0.00
Agriculture	-0.04	0.37	-0.10	0.92	0.21	0.42	0.51	0.61	1.39	0.26	5.40	0.00
Natural	-0.24	0.37	-0.66	0.51	0.34	0.42	0.81	0.42	0.59	0.25	2.38	0.02

II. Infection rates

	500m				1000m				5000m			
	Est.	SE	z	p	Est.	SE	z	p	Est.	SE	z	p

Intercept												
Urban	-0.04	0.27	-0.13	0.89	-0.34	0.27	-1.24	0.22	0.27	0.43	0.62	0.54
Agriculture	-1.04	0.37	-2.80	0.01	-1.14	0.36	-3.14	0.00	0.00	0.41	-0.01	0.99
Intercept	-1.89	0.36	-5.20	0.00	-1.89	0.33	-5.77	0.00	-1.88	0.38	-5.00	0.00
Urban	0.56	0.44	1.25	0.21	0.11	0.34	0.34	0.73	0.45	0.42	1.07	0.29
Natural	0.46	0.44	1.05	0.30	0.63	0.33	1.88	0.06	0.40	0.40	1.00	0.31
Intercept	-1.86	0.27	-6.87	0.00	-1.87	0.27	-6.88	0.00	-1.87	0.35	-5.36	0.00
Agriculture	-1.04	0.36	-2.87	0.00	-0.92	0.40	-2.31	0.02	0.77	0.57	1.36	0.17
Natural	-0.05	0.25	-0.20	0.84	0.18	0.31	0.58	0.56	0.83	0.57	1.47	0.14
