NOAA GRANT NUMBER: NA14NOS4820092

TITLE: Predictive modeling of mesophotic coral reef ecosystems throughout the Hawaiian Archipelago for conservation and management in the face of anthropogenic threats and future climate change

PRINCIPAL INVESTIGATOR: Dr. Robert Toonen

GRADUATE ASSISTANT: Lindsay Veazey

FUNDING PERIOD: Sep. 1, 2014 - August 31, 2015

Executive Summary

Using the archive of available video and photographic records from the Hawai'i Undersea Research Laboratory (HURL) and the Pacific Islands Fisheries Science Center (PIFSC), we developed a model to predict the occurrence of two dominant mesophotic coral genera, *Leptoseris* and *Montipora*, across the main Hawaiian Islands. The overall prediction success (73.6% and 74.3%, respectively) was relatively high, and these predictions were translated to spatially independent habitat suitability maps of the main Hawaiian Islands at 25 m² resolution. *Montipora* presence peaks in the middle mesophotic zone (50 - 80 m) in areas sheltered from high intensity winter swells, whereas *Leptoseris* tends to colonize steep, rugose, well-flushed areas in the lower mesophotic zone (> 80 m).

FINAL REPORT

Background

Tourism provides an estimated influx of more than \$10 billion to the Hawaiian economy each year, and many tourists come primarily to experience the islands' unique marine environment¹. Thus, understanding and maintaining the resilience of Hawai'i's reefs is critical. Sustained deterioration of marine ecosystem health worldwide suggests that critical gaps still exist in governmental management of ocean resources^{2, 3}. Marine ecosystems are faced with stressors such as coastal development, overfishing, introduction of alien species, pollution, nutrient and sediment runoff, and climate change^{4, 5, 6, 7}. Marine spatial planning (MSP) is a cost-effective, non-invasive, mathematically robust technique of projecting the effects of present-day activities on the health of marine organisms^{8, 9}.

Introduction

Mesophotic coral ecosystems (MCEs), located at depths of 30 - 180 meters, are an extension of shallow reefs and known to harbor many of the same species present at shallower depths as well as unique organisms native to this zone^{10, 11}. MCEs are primarily comprised of macroalgae, sponges, and hard corals that have adjusted or adapted to low light levels¹⁰.

Because of the challenges associated with research in this depth range, mesophotic research in Hawai'i has been conducted almost exclusively using data sourced from the Au'au Channel, Maui, a relatively calm, shallow, and more enclosed environment. The uniqueness of this habitat highlights the importance of creating a working predictive habitat suitability model

based on data from multiple sampled regions across Hawai'i to expand the scope and utility of such studies. Our study region encompasses the main eight Hawaiian Islands, and our observational data is sourced from the mesophotic zone along south O'ahu, southeast Kaua'i, and the Au'au Channel, Maui (Fig. 1).

In this study, we



Figure 1.The study domain, demarcated in blue, encompasses the mesophotic zone (30 - 180 m. in depth) of the lower main Hawaiian Islands. *In situ* observations are represented by black circles.

examined two types of error (false negatives and false positives) and analyzed our models without giving preference to either one. This approach is widely accepted as the best method of overall error minimization^{12, 13}. We propose implementation of a generalized linear model (GLM) to analyze ecological datasets for each coral genus (*Leptoseris* and *Montipora*). Because overall probability of coral occurrence is low in these data (0.052 and 0.042, respectively), we modified our model estimates using a rare events prior correction and Bayesian correction factor as proposed by King and Zeng (2001). To better interpret realistically low occurrence probability values generated by each model, we chose a probability (theta) threshold to transform the probability estimates to presence/absence values. This is standard practice when examining the results of a rare events logistic regression, but less common when performing an ordinary logistic regression¹².

Graduate Student Training

This project forms the basis of a Master's Thesis for GA Lindsay Veazey who has since submitted the manuscript for peer-review in the open-access journal *PeerJ* for subsequent publication. A copy of the manuscript in review is available on request, and will be freely accessible to all as soon as published.

Results

The *Leptoseris* model identified depth, slope, rugosity, and mean current velocity (northward/winter and eastward/summer) as variables that are influential in determining the distribution of *Leptoseris*. The *Montipora* model identified depth and winter significant wave height as variables that affect *Montipora* distribution.

The corrected *Leptoseris* model identified 71.7% of all true presences and 73.5% of all true absences, resulting in an overall predictive success of 73.6%. The overall predictive success of the *Montipora* model was 74.3%, with 73.6% of all presences and 74.7% of all absences properly identified. Model performance was confirmed using leave-one-out-cross-validation, which required 50% of the original dataset to be withheld and subsequently tested after the model was constructed using the remaining data.

All-island predictive maps were generated by each model (Fig. 2). Habitat suitability is depicted along a color gradient ranging from red (1; most suitable) to blue (0; least suitable). Full-page maps for each genus and island are available in Appendix I.

We also created maps of individual and summed predicted occurrence probabilities of both coral genera across the main Hawaiian Islands and ran a hotspot analysis using the ArcGIS Getis-Ord Gi* Hotspot Analysis tool. Our final maps show the results of our hot spot analysis across all islands (Fig. 3). Hotspots of habitat suitability for both coral genera are shown in red for areas of highest suitability and blue for areas of lowest suitability. A cell is identified as a hotspot when the sum of its value and the value of its neighbors is proportionally much higher or lower than the expected sum of all cells.

Mesophotic algae observations

Additionally, we constructed an inventory of mesophotic algae observations for south O'ahu and the Au'au Channel. We determined that the most appropriate representation of mesophotic algae in this project is via maps of observations of presence of the most dominant mesophotic algal communities (Appendix). The creation of this mesophotic algae map is the first of its kind in Hawai'i, and more observations can be added as future work progresses.

Management Implications Summary

The habitat preferences of mesophotic Montipora and appear distinct. Predicted *Montipora* prevalence across the mesophotic zone peaks at about 60 meters (median occurrence probability = 7.5%); *Leptoseris* occupancy peaks at about 100 meters (median occurrence probability = 7.5%). These predictions are fairly consistent with the inferences of Rooney *et al.* (2010), which parse mesophotic reefs into three distinct sections: upper (30 - 50 m.), branching/plate dominated (50 - 80 m.), and Leptoseris dominated (\geq 80 m.). The depth at which suitability peaks for Leptoseris occurs at a range where ridges and dropoffs are plentiful in our study region, and therefore is possibly prone to slight overestimation.



Figure 2. Modeled area of suitable habitat for *Leptoseris* sp. (top) and *Montipora* sp. (bottom) across the lower main Hawaiian Islands.



Figure 3. Mapped result of our Getis-Ord Gi* hotspot analysis performed for probability estimates of *Leptoseris* (top), *Montipora* (middle), and both genera (bottom) occurrence. A significant hotspot is ≤ -1.96 or ≥ 1.96 ; here, all hotspots are shown in red (≥ 1.96) or blue (≤ -1.96).

Scleractinians are able easily colonize environments that are both relatively calm and somewhat due to the larger amount of available surface area, and this positive correlation was reflected in our model. *Leptoseris* habitat preference was also positively associated with slope, which was not observed for *Montipora*. Corals which inhabit the upper mesophotic zone may be more susceptible to damage from debris displaced by high wave energy or current flow, and are therefore less likely to colonize steep slopes^{15, 16}. The deeper distribution of *Leptoseris* may

protect it from damage related to wave intensity, allowing it to freely colonize across steep slopes.

Our *Montipora* model was simpler than the *Leptoseris* model in that the only variable included other than depth was winter significant wave height. Though uncertainty was highest at lower values of significant wave height, *Montipora* demonstrated a preference in colonizing habitats that experience lower significant wave height during winter. Though mesophotic corals are generally thought to be excepted from the growth limitations faced by shallow water corals in regions of high wave energy, prolonged wave intensity as well as short-duration extreme storm event waves have been shown to negatively affect the colonization of upper mesophotic scleractinians, especially in sloping areas prone to debris avalanches^{15, 17, 18}. Continuation of this work might include a more in-depth examination of the relationship of this coral genus with the slope of available substrate and exposure to wave energy. We might expect the present-day distribution of these corals to shift as climate change spurs the formation of more frequent, intense storm events.

Substrate hardness, a variable known to influence coral colonization, was notably absent from each model. Substrate hardness values were derived from acoustic backscatter imagery readings. The resolution of these readings (50 m. x 50 m.) was not sufficiently detailed enough for purposes of this analysis. We noted plentiful coral colonization along larger surfaces like lava fingers, the hardness of which would be detectable by backscatter surveys, as well as across small rock fragments strewn across a sand flat, which would be obscured by the softness of the surrounding benthos. We can conclude that measurements of benthic hardness are not detailed enough for predictive modeling purposes at a 25 m² resolution.

The consistent identification of southern coastal areas as suitable is reliable, but the comparatively infrequent selection of northern coasts is likely due to the source of the modelbuilding observations. The vast majority of mesophotic exploration has been conducted along southern coastlines, which is often where waters are calmest in Hawai'i. It is speculated that because mesophotic corals are more shielded from winter long-period wave energy than their shallow water counterparts, they are able to flourish at depth along northern coastlines^{19, 20}. (Grigg 1998, Rooney et al. 2010). The addition of data sourced from northern expeditions would very likely improve predictive power of the model across north-facing coastlines. The ongoing supplementation of this database with observations of hard coral presence would be very beneficial to overall model success, especially in light of more recent research which recognizes numerous mesophotic scleractinians as "generalists" versus depth "specialists"^{17, 21}.

Future Directions

Because the scope of this study included all main Hawaiian Islands, we were constrained by the coarseness of available full-coverage environmental data. As we build on this analysis, we plan to use our maps to identify areas of interest for further study at higher resolution and to include additional variables currently only available in certain regions, such as light intensity and

temperature at depth. For example, our predictive and hotspot maps identify Penguin Bank (southwest Moloka'i) as particularly suitable for *Leptoseris* colonization, which has not been verified by video or photo records. High resolution backscatter data (1 m^2) exist for this region, and incorporation of these data into new analyses of subsets of our study area may refine our conclusions.

Date	Audience	Product
04/2015	40th Annual Albert J. Tester Memorial	15 minute oral presentation of work in
	Symposium at the University of Hawai'i at	progress
	Manoa	
08/2015	23rd Annual Hawai'i Conservation	15 minute oral presentation of completed
	Conference at the University of Hawai'i at	study
	Hilo	
12/2015	<i>Ecography</i> peer review	Submission of manuscript of findings titled
		"The implementation of rare events logistic
		regression to predict the distribution of
		mesophotic hard corals across the main
		Hawaiian Islands" – rejected without
		review due to limited geographic scope
12/2015	State of Hawai'i resource managers and	1 page managers' summary of findings and
	marine scientists	plans for continuing research
1/2016	The Department of Biology at the	Master's Thesis defense given in part to
	University of Hawai'i at Manoa	support L. Veazey's transfer to the Biology
		PhD program
1/2016	PeerJ peer review	Submission of manuscript titled "The
		implementation of rare events logistic
		regression to predict the distribution of
		mesophotic hard corals across the main
		Hawaiian Islands" – currently in review.

Communication and Outreach

We also created a 1-page information summary of the output of the results of this project (see page following the references) to highlight the primary findings of this work, and this document will be sent to the following resource managers as soon as we are able to provide the citation to the work currently under peer-review.

Name	Affiliation	Name	Affiliation
Bruce Anderson, Alton	Hawaii State	Gerry Davis, Liz Fairey, Malia	NOAA
Miyasaka, Brian	DAR	Chow, Danielle Jayewardene,	NCCOS,
Neilson, Russel Sparks,		Lance Smith, Bryan Costa, Matt	NMFS,
Bill Walsh, Maria		Kendall, Kimberly Puglise,	CRCP,
Carnevale		Randy Kosaki, Daniel Wagner	HIHWNMS,
			PIMINIM
Richard Pyle	Bishop Museum	Anthony Montgomery	USFWS
Josh DeMello	WestPac	Curt Storlazzi	USGS

REFERENCES

- 1. "Hawaii Tourism." Honolulu Civil Beat. Peer News LLC. Web. 01 Dec. 2013.
- Douvere, F. 2008. The importance of marine spatial planning in advancing ecosystem-based sea use management. Marine Policy 32(5): 762 - 771. doi:10.1016/j.marpol.2008.03.021.
- 3. Crowder, L. Norse, E. 2008. Essential ecological insights for marine ecosystem-based management and marine spatial planning. Marine Policy 32(5): 772 778. doi:10.1016/j.marpol.2008.03.012.
- 4. Ruiz, G., Fofonoff, P., Hines, A. 1999. Non-indigenous species as stressors in estuarine and marine communities: Assessing invasion impacts and interactions. Limnology and Oceanography 44: 950 - 972.
- Lenihan, H., Peterson, C., Kim, S., Conlan, K., Fairey, R., McDonald, C., Grabowski, J., Oliver, J. 2003. Variation in marine benthic community composition allows discrimination of multiple stressors. Marine Ecology Progress Series 261: 63 - 73.
- Adams, S. M. 2005. Assessing cause and effect of multiple stressors on marine systems. Marine Pollution Bulletin 51: 649 - 657.
- Crain, C., Kroeker, K., Halpern, B. 2008. Interactive and cumulative effects of multiple human stressors in marine systems. Ecology Letters 11: 1304 - 1315.
- Jackson, L., Trebitz, A., Cottingham, K. 2000. An Introduction to the Practice of Ecological Modeling. BioScience 8: 694 -706.
- Larsen, P., Barker, S., Wright, J. Erickson, C. 2004. Use of Cost Effective Remote Sensing to Map and Measure Marine Intertidal Habitats in Support of Ecosystem Modeling Efforts: Cobscook Bay, Maine. Northeastern Naturalist 11(2): 225 - 242.
- Lesser, M., Slattery, M., Stat, M., Ojimi, M., Gates, R., Grottoli, A. 2010. Photoacclimatization by the coral Montastraea cavernosa in the mesophotic zone: light, food, and genetics. Ecology 91:990 – 1003.
- Kane, C., Kosaki, R., Wagner, D. 2014. High levels of mesophotic reef fish endemism in the Northwestern Hawaiian Islands. Bull. Mar. Sci. 90:693 – 703. doi:10.5343/bms.2013.1053.
- Liu, C., Berry, P., Dawson, T., Pearson, R. 2005. Selecting thresholds of occurrence in the prediction of species distributions. Ecography 28: 385 - 393.
- Fielding, A. H., Bell, J. F. 1997. A review of methods for the assessment of prediction errors in conservation presence/ absence models. Environmental Conservation 24: 38 - 49.
- 14. King, G., Zeng, L. 2001. Logistic regression in rare events data. Political Analysis 9: 137 163.
- 15. Harmelin-Vivien M. L., Laboute, P. 1986. Catastrophic impact of hurricanes on atoll outer reef slopes in the Tuamotu (French Polynesia). Coral Reefs 5: 55 62.
- 16. Bridge, T., Guinotte, J. 2013. Mesophotic coral reef ecosystems in the Great Barrier Reef world heritage area: their potential distribution and possible role as refugia from disturbance. Research Publication no. 109. Great Barrier Reef Marine Park Authority. Townsville, QLD. 57 pp.
- 17. Kahng, S. E., Copus, J. M., Wagner, D. 2014. Recent advances in the ecology of mesophotic coral ecosystems (MCEs). Current Opinion in Environmental Sustainability 7: 72 81.
- White, K. N., Ohara, T., Fujii, T., Kawamura, I., Mizuyama, M., Montenegro, J., *et al.*, and Reimer, J. D. 2013. Typhoon damage on a shallow mesophotic reef in Okinawa, Japan. PeerJ 1: e151.
- 19. Grigg, R. 1998. Holocene coral reef accretion in Hawai'i: a function of wave exposure and sea level history. Coral Reefs 17: 263 - 272.
- Rooney, J., Donham, E., Montgomery, A., Spalding, H., Parrish, F., Boland, R., Fenner, D., Gove, J., Vetter, O. 2010. Mesophotic coral ecosystems in the Hawaiian Archipelago. Coral Reefs 29:361 367.
- Bongaerts, P., Frade, P., Hay, K., Englebert, N., Latijnhouwers, K., Bak, R., Vermeij, M., Hoegh-Guldberg, O. 2015. Deep down on a Caribbean reef: lower mesophotic depths harbor a specialized coral-endosymbiont community. Scientific Reports 5: 7652.

Mesophotic coral reef ecosystems (MCEs) occur between depths of 30 - 180 m, making them challenging to reach, and therefore historically understudied, because they fall between the maximum of SCUBA divers and the minimum typical working depth of submersible vehicles. Despite this paucity of studies, they are known to house considerable novel biodiversity and are expected to provide a depth refuge for shallow-water coral reef organisms in the face of global climate change (e.g., Bongaerts et al. 2010, Kahng et al. 2014). One of the challenges of managing such habitats is that we do not know where exactly they are found until a mission is sent to explore a given area with submersible, ROV or technical diving technologies. To assist in identifying MCE habitats, we developed predictive habitat suitability maps for two genera of mesophotic scleractinian corals (*Leptoseris* and *Montipora*) across the main Hawaiian Islands (Veazey et al., in review).

Using the archive of video and photographic records from the Hawai'i Undersea Research Laboratory (HURL) and the Pacific Islands Fisheries Science Center (PIFSC), we developed a model to predict the occurrence of these coral genera across the main Hawaiian Islands. The overall prediction success (73.6% and 74.3%, respectively) was relatively high, and these predictions were translated to spatially independent habitat suitability maps of the main Hawaiian Islands at 25 m² resolution (Figs. 1 & 2). *Montipora* thrives in the middle mesophotic zone in areas sheltered from high intensity winter swells, whereas *Leptoseris* tends to colonize steep, rugose, well-flushed areas in the lower mesophotic zone.

These models can be further improved with additional data and expanded to additional species to better understand the distribution of MCEs across the Hawaiian Archipelago. Such maps are expected to facilitate planning efforts by resource managers (e.g., support for a proposal that offshore construction activities occur in areas less likely to contain valuable and sensitive MCE communities), inform strategies for conservation, and supplement scientific dive planning to explore these important , but understudied, ecosystems.



References:

Bongaerts, P. T. Ridgway, E.M. Sampayo & O. Hoegh-Guldberg (2010). Assessing the 'deep reef refugia' hypothesis: focus on Caribbean reefs. Coral Reefs 29: 309 – 327.

- Kahng, S.E., J.M. Copus, & D. Wagner (2014). Recent advances in the ecology of mesophotic coral ecosystems (MCEs). Current Opinion in Environmental Sustainability 7: 72 81.
- Veazey, L., E.C. Franklin, C. Kelley, J. Rooney, L.N. Frazer, & R.J. Toonen (submitted). The implementation of rare events logistic regression to predict the distribution of mesophotic hard corals across the main Hawaiian Islands. *PeerJ* (reference to be included when available)

APPENDIX (detailed maps of predicted MCE coral distribution)

Mesophotic algae observation maps



Figure 4. Map of field observations of mesophotic algae in South O'ahu.



Figure 5. Map of field observations of mesophotic algae in the Au'au Channel.

Habitat suitability maps

Coefficient values from the rare events corrected models were used to create our allisland maps. Summary statistics for all variables used in the *Leptoseris* and *Montipora* rare events corrected models are included at the end of this section (Tables 2 - 3).

Ni 'ihau





Figure 6. Modeled area of suitable habitat for *Leptoseris* sp. (top) and *Montipora* sp. (bottom). Coverage area of *Leptoseris* around Ni'ihau above the theta threshold (0.067) is approximately 1180 km². The *Montipora* model was not able to identify habitat around Ni'ihau above the theta threshold (0.0625). Habitat suitability is depicted along a color gradient ranging from red (1; most suitable) to blue (0; least suitable).

Predicted coverage of *Leptoseris* spanned across all coasts of Ni'ihau at depths ranging from 31 - 180 meters. Southeastern Ni'ihau was identified as particularly suitable for both *Leptoseris* and *Montipora* corals (Fig. 12). Average predicted probability of *Montipora* occurrence was 1.3%, though the model was not able to identify regions of suitable habitat above

the theta threshold. Average predicted probability of *Leptoseris* occurrence across Ni^cihau was 3.9%.



Kaua'i



Figure 7. Modeled area of suitable habitat for *Leptoseris* sp. (top) and *Montipora* sp. (bottom). Coverage of *Leptoseris* around Kaua'i above the theta threshold is predicted across 2378 km², while the *Montipora* model identified approximately 45 km² of suitable habitat above the theta threshold. Habitat suitability is depicted along a color gradient ranging from red (1; most suitable) to blue (0; least suitable).

The eastern and southern coast of Kaua'i were selected most suitable for *Leptoseris*, while the southwestern coast was suitable for both *Montipora* and *Leptoseris* (Fig. 13). Mean *Leptoseris* occurrence probability was estimated to be 8.5%, and average occurrence probability of *Montipora* was 0.7%.





Figure 8. Modeled area of suitable habitat for *Leptoseris* sp. (top) and *Montipora* sp. (bottom) across O'ahu. The *Leptoseris* model identified approximately 7738 km² of area above the

The model habitat above suitability across all except for northwestern Montipora identified habitat along and western 14). Mean occurrence was 7.8%. suitable habitat entire zone with a meters in

Mean occurrence was 0.1%. *Montipora* ranged from meters with 58.5 meters southern and coasts of identified as for colonization.



Leptoseris identified the threshold O'ahu coasts the shore; the model suitable the southern coasts (Fig. predicted of Leptoseris Predicted Leptoseris spanned the mesophotic mean of 86 depth.

predicted of *Montipora* Suitable habitat 48.2 - 68.4 a mean of in depth. The western Oʻahu were most suitable *Montipora*

(Maui, Molokaʻi,

Maui Nui Lānaʻi, Kahoʻolawe) **Figure 9.** M Nui. The *Le*, *Montipora* r a color grad

Mean occurrence of was 6.9%. suitable habitat entire zone with a meters in Southwestern central Au'au western were very suitable habitat.

Mean occurrence of was 1.4%. *Montipora* from 40 with a mean in depth. The of the Au'au identified as for *Montipora*



tom) across Maui ity threshold. The y is depicted along

> predicted *Leptoseris* Predicted *Leptoseris* spanned the mesophotic mean of 75.6 depth. Moloka'i, the Channel, and Kaho'olawe identified as *Leptoseris*

predicted *Montipora* Suitable habitat ranged 76.3 meters of 61.1 meters western coast Channel was most suitable habitation.

Hawaiʻi





Figure 10. Modeled predicted distribution of *Leptoseris* sp. (top) and *Montipora* sp. (bottom). *Leptoseris* model identified approximately 3407 km² of area above the suitability threshold. The *Montipora* model identified 488 km² of habitat above the threshold. Habitat suitability is depicted along a color gradient ranging from red (1; most suitable) to blue (0; least suitable).

Suitable *Leptoseris* habitat was identified along all coasts and all depths of the mesophotic zone, and it was particularly concentrated along the eastern and western coastlines. Mean probability of *Leptoseris* occurrence was 3.5%.

Mean probability of *Montipora* occurrence was 0.6%. The model identified suitable habitat concentrated along the north Kona and Kohala coasts and across depths ranging from 46.2 to 70.1 meters (mean = 100.1 m.).

l ris)	Statistic type	Variable				
Model (<i>Leptose</i> i		Depth (m.)	Mean current velocity (N/S) (m/s)	Mean current velocity (E/W) (m/s)	Slope (degrees)	Rugosity
Training Model	mean	77.449	-0.055	-0.026	3.900	0.0009
	st. dev.	24.807	0.141	0.086	5.785	0.002
Hawai'i	mean	110.096	0.102	0.027	4.942	0.001
	st. dev.	36.323	0.193	0.107	6.475	0.006
Maui Nui	mean	87.618	-0.080	-0.089	2.420	0.0004
	st. dev.	38.941	0.140	0.206	3.781	0.002
Oʻahu	mean	81.000	-0.112	-0.065	3.863	0.0007
	st. dev.	34.050	0.160	0.185	5.160	0.003
Kauaʻi	mean	73.942	-0.039	-0.072	4.495	0.001
	st. dev.	31.917	0.160	0.251	5.963	0.004
Niʻihau	mean	67.323	-0.063	-0.098	4.008	0.0009
	st. dev.	29.252	0.146	0.108	6.123	0.004
All islands (avg.)	mean	84.000	-0.038	-0.059	3.946	0.0008
	st. dev.	34.097	0.160	0.171	5.500	0.004

Table 2. Summary statistics for variables included in each *Leptoseris* rare events corrected model, delineated by island.

l ra)	ype	Variable		
Model (<i>Montipo</i>	Statistic t	Depth (m.)	Winter significant wave height (m.)	
Training Model	mean	78.256	0.909	
	st. dev.	25.145	0.460	
Hawai'i	mean	110.096	1.718	
	st. dev.	36.323	0.619	
Maui Nui	mean	87.618	1.706	
	st. dev.	38.941	0.690	
Oʻahu	mean	81.000	2.213	
	st. dev.	34.050	0.494	
Kauaʻi	mean	73.942	2.135	
	st. dev.	31.917	0.349	
Niʻihau	mean	67.323	1.757	
	st. dev.	29.252	0.315	
All islands (avg.)	mean	84.000	1.906	
	st. dev.	34.097	1.234	

Table 3. Summary statistics for variables included in each

 Montipora rare events corrected model, delineated by

 island.