TESTING SPATIAL MANAGEMENT STRATEGIES FOR HAWAII'S FUTURE REEFS: A BIOPHYSICAL, METACOMMUNITY APPROACH

By

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ABSTRACT

Coral reefs are invaluable resources in tropical communities, and support the cultural and substantial livelihoods of millions of coastal peoples. Reefs are home to a massive proportion of earth's biodiversity, and form the basis of commercially valuable fisheries and tourism industries. However, reefs are globally in decline, and it is in the interest of marine resource managers to understand and modulate impacts of climate- and human-induced effects on the continued resilience of their reef ecosystems. Simulation models have proven to be useful, though not perfect, tools to test and evaluate potential futures of reef ecosystems at a variety of spatial scales. These are most effective when incorporating a broad set of biological, climactic and environmental data, and can be adapted to various regions. This thesis presents the development, validation, and application of a pre-existing biophysical coral reef model, CORSET (Coral Reef Scenario Evaluation Tool) to a novel system, the Main Hawaiian Islands (MHI). The model was originally developed by Jessica Melbourne-Thomas and colleagues at the University of Tasmania as a portable framework to address biophysical processes on coral reefs across multiple spatial scales[1]. The model incorporates local ecology, larval connectivity, and anthropogenic and environmental forcings across an array of differential equations, run on a desktop computer and visualized using spatial or graphical software. It is a decision support tool for visualizing reef futures at regional scales in the order of 10^2-10^3 km. This study applies and demonstrates the portability of the CORSET model, and applies a test-case to examine potential reef scenarios under alternative climate, land-use and fishing protection regimes. The results hold implications for simulation testing in reef ecology and decision-support for marine fisheries management. The study conclusion also provides simulative evidence against the common paradigm that top-down management strategies will be the most effective in preserving coral cover.

KEYWORDS

coral reefs, spatially explicit, ecosystem modeling, fisheries, resource management

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Thanks as well to members of the Franklin Lab, especially Zack Oyafuso, who completed the original model parameterization and provided useful advice in the analytical stage of the project. Of course, a large thanks to Jess Melbourne-Thomas herself for being responsive and eager to share figures and advice regarding the revitalization of the CORSET model for this project.

A warm mahalo to my loving, supportive family and Hawaiian o'hana. To my partner, Oscar, *gracias y te quiero*.

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FIGURES INCLUDED IN THE MANUSCRIPT

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GLOSSARY

The following modeling terms are used throughout the thesis and are defined here for the reader's convenience. Adapted from Melbourne-Thomas (2010)[2]

Accuracy: The ability for a model to reproduce empirically-observed values for a given system when parameterized to the system at hand.

Calibration: an attempt to find the best accordance between modeled and observed data by variation of some selected parameters.

Complex system: Refers to systems that are comprised of a large number of interacting components. Complex systems are characterized by emergence (i.e. system-level properties that cannot be predicted from the properties of individual components) as well as non-linear behaviors and self-organization.

Connectivity: Refers to the rate of exchange of individuals between populations, driven largely by processes that influence larval dispersal. Connectivity can also refer to transport of suspended organic matter or dissolved nutrients.

Functional group: A classification of organisms based on morphological, physiological, behavioral, biochemical, or environmental responses, and/or on trophic criteria.

Instantiation: A term used to denote a particular 'instance' of a model, and/or to the procedure for creating such an instance. The instantiation procedure for models in this thesis involves parameterizing biophysical processes, creating a gridded basemap which identifies the location of coral reefs, and formatting connectivity information so that it is compatible with the model framework.

Nutrification: An increase in the flux of nutrients into coastal waters (as opposed to eutrophication, which is an ecological process). Nutrients that typically enter coral reef systems are inorganic and organic forms of nitrogen and phosphorus, including nitrate, ammonium, soluble reactive phosphate, and dissolved organic complexes that can be re-mineralized into organic forms.

Precision: Generally, the level of confidence of model outputs for a given time step or region.

Scenario: A plausible story about how the future might unfold, constructed using models of real systems and information on current and past conditions.

Sedimentation: The import and deposition of suspended sediments into coastal marine systems (mostly via rivers and terrestrial runoff). In the models presented here, sedimentation is represented as the eco- logical effects of sediment deposition on coral growth, death and reproductive success.

Validation: A comparison between model predictions and empirical observations

CONTEXT OF THE THESIS

CORAL REEF ECOSYSTEMS AND DECISION SUPPORT TOOLS

Coral reefs are traditionally robust ecosystems that provide food, storm shelter, and economic value to coastal communities worldwide. They support extensive biodiversity of marine life, acting as crucial spawning grounds and refugia for juvenile organisms. Coral reefs are globally in decline, with trajectories further threatened by disease, pollution, climate change, overfishing, and ocean acidification[3–5]. While these concerns are baleful in Southeast Asia and the Caribbean Basin, the state of Hawaiian coral reefs is relatively good[6,7], with the effects of shoreline development less detectible relative to natural factors that contribute to community structure. Among these, wave action and bleaching events are most influential on community composition, limiting assemblages to a few hardy species[8–10]. Nevertheless, the development of management strategies that are effective under better- and worser-case climactic scenarios is crucial for the continued resilience of coastal ecosystems and the populations that rely upon them. A major challenge to marine environmental decision-making in the face of climate change and anthropogenic influence is deciphering the contribution of complex ecosystem dynamics to environmental resilience across broad geographic scales. Additionally, prior or ongoing studies have limited their focus to impacts on coral species alone, and a limited set of environmental stressors such as seawater temperature and acidification[11,12]. Ideally, such models incorporate a broad set of biotic and environmental data, and enable managers to "test" certain management scenarios against inevitable changes in ocean chemistry, storm events and temperature.

STUDY SITE

The state of Hawaii, an island archipelago of eight main islands situated in the Central Pacific, is home to 1.42 million people. The landscape is largely varied, with only 6.1% of land area supporting dense populations (such as Waikiki beach on Oahu's south shore) and others (such as the Hilo side of the Big Island of Hawaii) more sparsely populated, with large land areas dedicated to agriculture. Regardless, significant swaths are subject to intensive urbanization, tourism development, and high fluxes in population density.

The island chain is largely supported by its burgeoning tourism industry, which attracts millions per year to its beaches, tropical climate, and seafood cuisine. The Main Hawaiian Islands (MHI) have been fished by recreational and subsistence-based fishermen for centuries, and more recently by commercial enterprises who exploit the growing human population and associated markets. While the MHI aren't explicitly overfished, the catch composition of commercial endeavors have shifted towards lower—valued species, such as goat and surgeonfishes[8], a result possibly exacerbated by non-existent recreational fishing license protocols, and the continued allowance of SCUBA-supported spearfishing[13,14]. A recent report by the National Oceanographic and Atmospheric Administration indicated that U.S. citizens value the protection of Hawaii's reef ecosystems alone at over $33 billion[15]. Clearly, effective management of coral reefs from both an ecological and human standpoint is of large economic concern. A scenario-based, decision-support tool that incorporates spatial aspects of ecosystem forcings and climactic and human events would enhance our ability to test and choose appealing management strategies for the state on a regional basis.

HUMAN-ENVIRONMENT INTERACTIONS

The ecosystem services upon which the Hawaiian people and visitors depend are intimately connected to coastal conditions. Reefs and reef-based fisheries are invaluable resources for Hawai'i's culture, recreation, research and economy. Understandably, near-shore ecosystem dynamics are confronted by anthropogenic activities, including resource extraction, destruction, and pollution from development. Unlike other tropical reef systems such as the Caribbean, the Hawaiian coral community appears to be in an intermediate state[6], with lower levels of degradation in the context of less-than-detectable anthropogenic impacts. This is good news, but doesn't negate the importance of ensuring continued reef resilience nor identifying potential sensitivities ("tipping points") for reef trajectories in the decades to come. While humans cannot control the onset of climactic upheaval, e.g. the frequency and intensity of bleaching events, such events can be modulated by human actions that exert stress upon the affected reef system[16,17]. For this reason, the exploratory phase of this study focuses on bleaching-fishing dynamics, to investigate how – or if – variations in fishing pressure may modulate reef recovery trajectories in the context of bleaching events and land-use chages.

MODELS IN REEF ECOLOGY

The construction and application of models of the natural world can aid managers and researchers in identifying the likelihood of future outcomes, and the tradeoffs of given management regimes. Simulative models of reef ecosystems have been used to evaluate ecological responses to a myriad of disturbance events, including fishing pressure, coral bleaching, invasion by alien species, and nutrient loading[18,19]. Coral reefs are notably difficult to model, considering the complexity of the socio-ecological relationship between reef systems and coastal communities, and the varied scale at which ecosystem processes (e.g. larval recruitment, fishing, grazing) take place. Despite such challenges, many studies have attempted to implement informative models for reef systems, considering the risk of continued degradation and uncertainties posed by climate change[20,21]. However, prior or ongoing studies have limited their focus to impacts on coral species alone, and a limited set of environmental stressors such as seawater temperature and acidification[12,22].

There is a clear need for coherence in our approach to preserve reef function and resilience. While countless studies have documented the degradation of reef ecosystems, a smaller number have identified management approaches that "worked", for example, by restoring previous levels of herbivore biomass[23]. Management development efforts often involve the application of spatial fishing closures, which are contentious in that they may be a perceived threat to the local economy. Strong management will arise from supportive tools that illustrate and reinforce our understanding of reef dynamics under threat[19,24]. A predictive, decision-support model should include a broad set of spatial, ecological, and climactic factors unique to the system of interest; the incorporation of spatial dynamics addresses uncertainty regarding whether reefs will exhibit spatial heterogeneity in their trajectories. Finally, such a model emerges as a decision-support tool as it provides the capacity to test management regimes in the context of climate change. Such a model, the Coral Reef Scenario Evaluation Tool (CORSET), has been developed and instantiated for both the Meso-American Reef (MAR) and South China Sea (SCS) regions. This model is novel in that it accounts for the many scales at which reef ecosystem processes take place; is comprised of a "bottom-up" structure wherein complex behaviors are not pre-programmed, but emergent[2]; and highly portable to new systems.

APPROACH

The objective of this thesis is to develop and evaluate an application of the CORSET tool to investigate reef trajectories in the MHI under a suite of climate and ecological scenarios, with emphasis upon changes in the removal of herbivore biomass and the frequency of thermal anomalies. The results, in addition to projected conclusions described in this manuscript, will be informative maps that will inform management and policy activities across the archipelago.

Chapter 1: *Development, Validation and Sensitivity Analysis of a Regional-Scale Biophysical Model of Coral Reefs in the Main Hawaiian Islands* develops a third instantiation of the CORSET model for the Main Hawaiian Islands (MHI), tests its validity and examines the effects of sensitivity upon model behavior. We investigate responses in coral community composition to extreme parameter values and varied temporal resolution. Our findings corroborate those for the initial instantiation of the model, and underscore the high-leverage nature of coral and fish fecundity, growth and death rates for community stability. It also demonstrates CORSET's portability. These findings have implications for sensitivity and error in predicting reef outcomes at the regional management scale.

Chapter 2: *Predicting climate impacts on tropical fisheries: are contemporary spatial management strategies sustainable?* applies the instantiation to the MHI archipelago to a suite of scenarios, with the intention of modeling dynamics between bleaching events and the allocation of no-take marine protected areas within reef systems. The incorporation of spatial dynamics addresses uncertainty regarding whether reefs will exhibit spatial heterogeneity in their trajectories. We find that the establishment of MPAs increased both biomass and catch of reef fish for lower functional groups. MPAs also 'rescued' herbivore populations from collapse in simulations of increased nutrient pollution. However, even extreme degrees of fishing protection are insufficient to protect higher trophic groups, and no scenario evaded the decimation of coral cover. This study has implications for spatial management of tropical fisheries worldwide and provides a portable framework for strategy testing at the regional scales. It also provides simulative evidence against the common paradigm that top-down management strategies will be the most effective in preserving coral cover. Finally, the model emerges as a decision-support tool as it provides the capacity to test management regimes in the context of climate change.

CHAPTER 1: DEVELOPMENT, VALIDATION AND SENSITIVITY ANALYSIS OF A REGIONAL-SCALE BIOPHYSICAL MODEL OF CORAL REEFS IN THE MAIN HAWAIIAN ISLANDS

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coral reefs, spatially explicit, ecosystem modeling, sensitivity

ABSTRACT

In any modeled system, parameter sensitivity and model accuracy can dictate the behavior, computational efficiency, and presumed validity of model projections. They are two important subjects of analysis for the creation of robust yet portable models. We develop and validate a novel instantiation of a regional-scale biophysical model of coral reef systems for the Main Hawaiian Islands (MHI) and evaluate several aspects of model behavior: a sensitivity analysis to temporal, spatial, and larval connectivity settings and an identification of high-leverage parameters coupled with the portability of parameter influence across low- and high-disturbance regimes. While such analysis is typically confined to examining the response of single state variables, such as benthic cover, our approach uses multivariate community composition as a response to modeling simulations**.** Our results suggest that the model is effective in producing accurate community compositions at the regional scale. Sensitivity analyses revealed that generally the same ecological parameters, namely coral and fish growth and death rates, are of high importance in both instantiated regions. Coral growth, fecundity and death rates are instrumental in determining whether communities undergo a phase shift or recovery under a high-impact bleaching scenario. These findings support further exploration of the CORSET model as a decision-support tool for the MHI, specifically for scenarios that may impact coral resilience and the death rates of tropical reef fish populations.

INTRODUCTION

Coral reefs are globally in decline, with trajectories further threatened by disease, pollution, climate change, overfishing, and ocean acidification[3–5]. A major challenge to marine environmental decision-making in the face of climate change and anthropogenic influence is deciphering the contribution of complex ecosystem dynamics to environmental outcomes across broad geographic scales. Governments and agencies tasked with managing reef resilience benefit from decision-support tools that can estimate changes to coral and fish populations in their region. Ideally, such models incorporate a broad set of biotic and environmental data, and enable managers to “test” certain management scenarios against inevitable changes in ocean chemistry, storm events and temperature.

Models have a long history of application to ecological systems, as they are useful for evaluating hypotheses regarding ecosystem trajectories or the relative contribution of ecological parameters to system behavior. While it is impossible to identify the single best model for a system, as ecosystems are inherently open and stochastic[25], researchers often strive for the most simple yet predictive model construct. Sensitivity analysis (SA) is the process by which we identify the most influential parameters to a model’s behavior, and subsequently draw conclusions about the system as a function of those parameters. In the marine environment, where organisms are subject to a fluid, variable, and spatially expansive set of environmental conditions, the importance of identifying the most predictive measures of ecological outcomes is ever more important.

The selection of appropriate temporal and spatial scales for an ecosystem model depends on the management question at hand; a sensitivity analysis can indicate at which resolution(s) the most variability occurs, which can in turn be compared to empirical expectations of the model system. This study instantiates and performs a set of sensitivity characterization procedures on a regional-scale, biophysical model of a reef ecosystem for the Main Hawaiian Islands (MHI). Following Klepper (1997)[26] and Melbourne-Thomas et al. (2011)[27], we used reef community composition, visualized in multivariate space, as the response variable to forcing parameters described below. This enables us to depict the "reef state" -- a composite of many variables – as an average across all reef cells in the domain as a function of various parameter selections.

Coral Reef Scenario Evaluation Tool (CORSET)

This study develops, validates, and characterizes the sensitivity and accuracy of a new instantiation of the Coral Reef Scenario Evaluation Tool (CORSET)[27] to the Hawaiian Archipelago, a chain of eight islands in the Central Pacific. CORSET was developed by Jessica Melbourne-Thomas and colleagues at the University of Tasmania as a portable framework to address biophysical processes on coral reefs across multiple spatial scales[1]. The tool is implemented in the open-source object-oriented Python Programming Language version 2.5[28]. While originally developed and parameterized for applications on Indo-Pacific and Meso-American reefs, CORSET is readily adaptable to perform scenario testing throughout the Hawaiian Archipelago.

The model is comprised of four components: local ecology, larval connectivity, and anthropogenic and environmental forcings (Figure 1). CORSET uses a 'functional group' approach to model interactions between two types of corals (brooding and broadcast spawning species), two types of algae (fleshy and foliose macroalgae, and turf algae), herbivorous fish, small-to-intermediate sized piscivorous fish, large piscivorous fish, and sea urchins. Benthic covers of coral and algae, and the biomasses of fish and urchins are modeled in each reef cell of a gridded base-map using a weekly time step. Parameters that describe local-scale ecological processes are selected at random from predefined, uniform ranges derived from empirical observations. The local-scale ecological model used in CORSET is a mean-field model that describes average interactions between benthic and consumer functional groups, which are coupled across subregions by larval dispersal. This structure renders CORSET as stochastic, with the inclusion of natural disturbances such as hurricane, disease, bleaching events, and direct human impacts (nutrification, fishing, and sedimentation).

CORSET models the dispersal and settlement of coral, reef fish and urchin larvae via matrices of transition probabilities between source and sink locations in the model domain. This is the singular instance of spatial connectivity within the model; it does not model movement of mature fish between cells.

Connectivity information is translated into recruitment dynamics in CORSET by:

(i) Accumulating larval production (from spawning events) from all reef cells in each reef polygon;

(ii) Modeling larval dispersal between polygons using information from Lagrangian stochastic particle tracking models[29]; and

(iii) Dividing larvae that arrive at a particular sink polygon equally between all adjacent reef cells.

The CORSET software partitions fishing pressure (*f*) amongst three functional groups: large piscivorous fish, small piscivorous fish, and herbivores, such that ($\rho H + \rho Ps + \rho Pl = 1$). Fishing pressure is modeled as a decrease in fish biomass that is apportioned between herbivorous, small-to-intermediate piscivorous and large piscivorous fish groups, which can vary through each time step. The CORSET software allows us to specify fishing pressure at the subregional level for each year, or to allow it to vary randomly across a specified range at the regional scale.

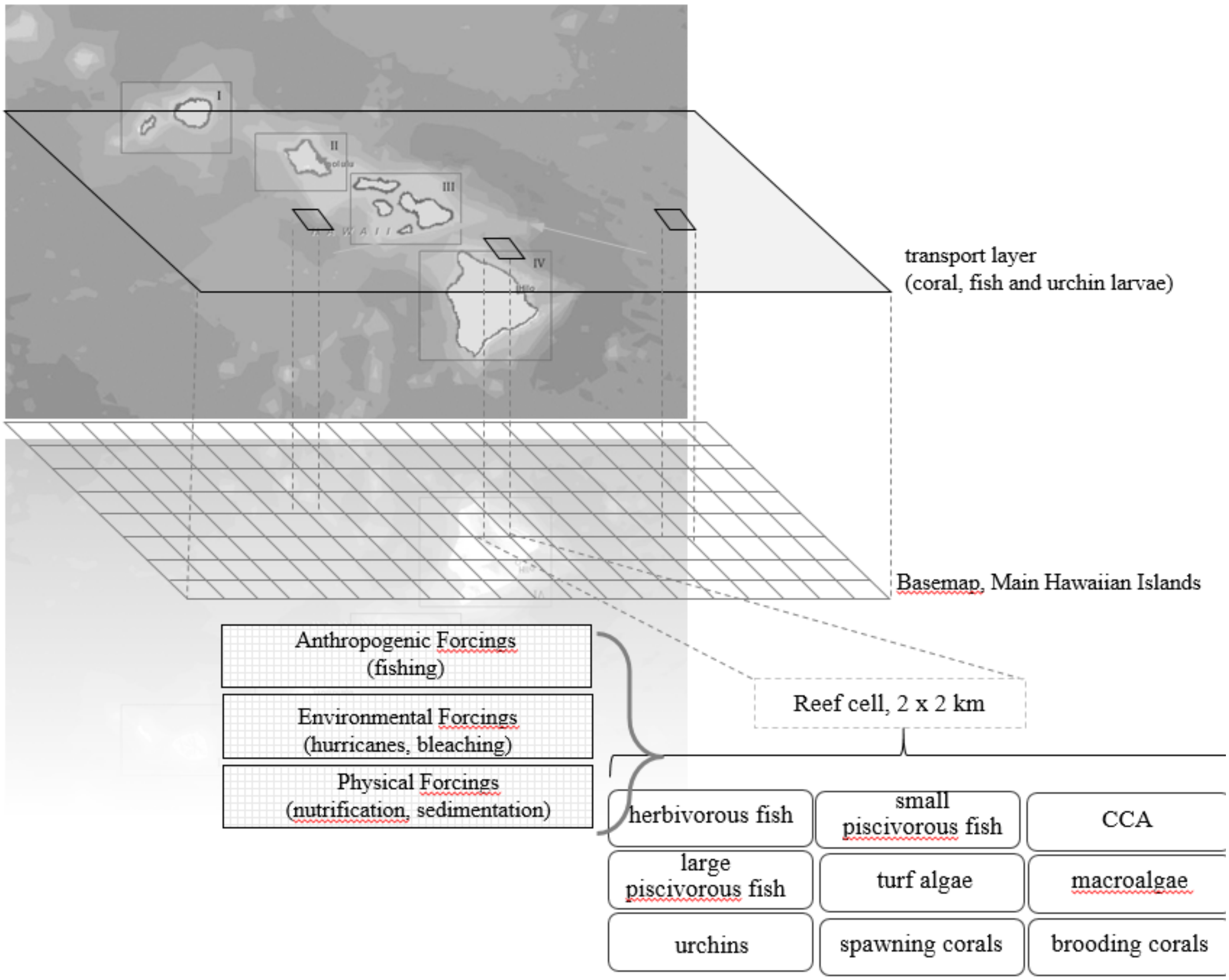


FIGURE 1. SCHEMATIC OF STRUCTURE AND FUNCTION IN CORSET. MEAN-FIELD EQUATIONS DESCRIBING LOCAL-SCALE INTERACTIONS BETWEEN BENTHIC AND CONSUMER FUNCTIONAL GROUPS (SEE APPENDIX A) ARE INSTANTIATED IN EACH REEF CELL OF A GRIDDED BASE-MAP. REEF CELLS ARE CONNECTED THROUGH LARVAL TRANSPORT, WHICH IS DEFINED BY CONNECTIVITY MATRICES OF TRANSITION PROBABILITIES FOR EACH OF (SPAWNING) CORAL, FISH AND SEA URCHIN LARVAE. FISHING, NUTRIFICATION AND SEDIMENTATION ARE MODELED AS EXTERNAL FORCINGS.

CORSET models the effect of nutrification specifically as an increase in the scaling parameter for macroalgal growth, and a depression of successful coral larval recruitment. It does not directly model impacts of increased nutrification on fish community structure or predative ability. Conversely, sedimentation forcings enact a scaled increase of coral mortality in affected cells. Hurricane events, which are more prevalent in Caribbean systems and thus applied more thoroughly in those instantiations, effect acute mortality of coral cover similarly to bleaching events. The user may elect to implement hurricanes (of customizable damage), sedimentation or nutrification events within specified reef cells and given years; alternatively, one can select "no forcing", which disables any effects from these events. Readers are referred to Appendix A, which describes the local-scale model's development, assumptions, equations, and initial parameters used for the Mesoamerican and Indo-Pacific instantiations of CORSET.

METHODS

MODEL INSTANTIATION

BASEMAP

We developed a gridded basemap consisting of four subregions: Kaua'i – Ni'ihau; O'ahu, Maui Nui, and Hawai'i (also known as the Big Island). The spatial extent of this instantiation was 3,263,632 km^2 and a total reef area of 1,342 km^2 was modeled. The rationale for the subregional delineation is two-fold: firstly, geographically-designated subregions are ideal for organizing management efforts; secondly, there is additional genetic evidence that these regions maintain genetic barriers to dispersal among them[30]. However, subregional designation has no bearing on the behavior of the model; they are simply organizational units for forcing activities.

The domain was represented in two resolutions: 2km x 2 km, and 4 km x 4 km. The 2 km x 2 km resolution was used for the all validation and sensitivity procedures; a subsequent analysis compares model trajectories between the three resolutions.

LOCAL-SCALE ECOLOGICAL PARAMETERS

We modeled local-scale ecology through CORSET's dynamic difference equation array for nine functional groups: brooding corals, spawning corals, macroturf, macroalgae, grazed epilithic algal communities (EAC), herbivorous fish, small-to-intermediate piscivorous fish, large piscivorous fish, and sea urchins. Parameter inputs, in the form of .txt files, were modified based on empirical data gathered from field and remote-sensing studies throughout the Hawaiian Islands. In the absence of such data, range substitutions were made from previous instantiations' parameratizations, namely in the Indo-Pacific. A list of initial values, their description and sources are in Table 1. Empirical % coral cover values were partitioned as 75% broadcast spawning corals (producing and releasing gametes over a broad geographic area), and 25% brooding corals.

	Parameter	Definition	Source(s)	Kauai –Niihau	Oahu	Maui Nui	Hawaii
				Subregion			
Modeled Domain (km^2)		Spatial extent of modeled reef cells		1600	1440	3184	2912
				Estimated Values ± standard error			
HISTORICAL (ca. 1965)	Mean Coral Cover	Average % cover. Calculated as 20% increase over present-day	31	9.3 ± 1.86	14.28 ± 1.32	23.56 ± 2.44	29.52 ± 1.08
	Cb	*brooding corals, mean % cover ca. 1965*		*2.32*	*3.57*	*5.89*	*7.38*
	Cs	*spawning corals, mean % cover ca. 1965*		*6.98*	*10.71*	*17.67*	*22.14*
	T	Mean % cover of macroturf	31–33	51	32	17	17
	M	Mean % cover of macroalgae	31–33	5	12	11.5	<2
PRESENT – DAY (ca. 2015)	Mean Coral Cover	Average % cover	32,33	7.75 ± 1.55	11.9 ± 1.1	19.6 ± 2.03	24.6 ± 0.9
	Cb	*brooding corals, mean % cover*	8,31–33	*1.94*	*2.97*	*4.90*	*6.15*
	Cs	*spawning corals, mean % cover*	8,31–33	*5.81*	*8.92*	*14.72*	*18.45*
	T	Mean % cover of macroturf	32,33	51	32	39	56
	M	Mean % cover of macroalgae	32,33	11	12	11.5	<2
CONSUMER PARAMETERS	H	herbivorous fish, kg km^{-2}	33	31700			
	Ps	small piscivores, kg km^{-2}	33	1800			
	Pl	large piscivores, kg km^{-2}	33	1800			
	U	Urchins, kg km^{-2} [3]	33	99			

TABLE 1. INITIAL VALUES USED IN LOCAL SCALE MODEL VALIDATION FOR MAIN HAWAIIAN ISLANDS. PARAMETERS ARE ESTIMATED FROM EMPIRICAL SOURCES WHERE AVAILABLE.

LARVAL CONNECTIVITY MODEL

ENVIRONMENTAL FORCINGS

Here, "forcings" refers to modeled changes in fishing pressure, hurricane, disease and bleaching events, nutrification[34], and sedimentation. Hurricane, sedimentation and nutrification disturbances are modeled as external forcings that affect benthic and consumer groups, via changes in growth, mortality and recruitment parameters. We gleaned a range of proportional mortality values from historical bleaching events within the Main Hawaiian Islands, which range from 5% to a maximum of 15% -- the percentage indicating the proportional loss of coral cover attributable to a bleaching event alone[4,12,35]. We validate the model using real-world bleaching events from the last five decades using this mortality range.

Hurricane events were not forced during the validation aspect of this study, as they are not considered a strong ecological driver in this region[36,37], especially relative to Caribbean reefs[6,38–40]. Nutrification and sedimentation impacts were also not modeled as forcing events in checking for model accuracy. Elementary effects analyses of nutrification and sedimentation for the complex integrated model from which CORSET originated[41] indicate that nutrification exhibits a range of effects upon parameter outcomes; the largest being a positive effect upon macroturf growth. Its effects upon coral cover are negative but only moderately so[41]. Sedimentation enacts only small negative effects on average to all parameters besides urchins, which constitute a much smaller fraction of the Hawaiian benthos than in other regions[42]. Parameters representing the scaling of turf and coral growth due to nutrification and sedimentation are detailed in Appendix F, which, along with hurricane damage, were allowed to vary randomly within their ranges for the parameter sensitivity analysis.

ANTHROPROGENIC FORCINGS

For validation procedures, present-day fishing catch was made accessible by the State of Hawai'i Department of Aquatic Resources, in tabular and spatial form**.** The data from 2003 - 2011 were subset for coastal (<2 nm from shore) fishing polygons, from which a fishing pressure parameter (kg km^{-2} yr^{-1}) was calculated for each subregion (Appendix E). We estimated historical commercial and recreational catch from prior reports[43], modeling changes as a linear, proportional sub-regional increase in fishing pressure (in kg km^{-2}) from 1965 – 2015. This per-capita interpolation method is a desirable alternative to the unsatisfactory method of assuming "zero catch" for years wherein data is absent[44,45]. In all sensitivity analyses, fishing pressure was assigned a value of zero throughout the model run.

MODEL VALIDATION

MODEL STABILITY

We performed a model validation to test whether the calibrated model was able to produce stable long-term (100-year) trajectories in the absence of external forcings, and to examine accuracy of the model at matching observed community composition measures for the period from 1965 through 2010. For both procedures, we used initial values for benthic and consumer percent cover and biomass derived from empirical observations wherever possible. A list of initial values, their description and sources are found in Table 1.

MODEL ACCURACY

To test whether the model could accurately reproduce observed values for current community composition, we simulated real-world coral bleaching events at years 1996, 2002 and 2014, with proportional damage ranging between 0.05 and 0.15%. Additionally, best estimates for historical and current fishing pressure were incorporated into model runs as a linear increase in fishing pressure across all functional groups. For validation procedures, present-day fishing catch was made accessible by the State of Hawai'i Department of Aquatic Resources, in tabular and spatial form**.** The data from 2003 - 2011 were subset for coastal (<2 nm from shore) fishing polygons, from which a fishing pressure parameter (kg km^{-2} yr^{-1}) was calculated for each subregion (Appendix E). Historical commercial and recreational catch was estimated from prior reports (Pooley 1993). We modeled this as a linear, proportional sub-regional increase in fishing pressure (in kg km^{-2}) from 1965 – 2015, with 10 Monte Carlo simulations. In all sensitivity analyses, fishing pressure was assigned a value of zero throughout the model run.

For robust comparision, we normalized empirical values from benthic and consumer reef survey data collected throughout the MHI over the last 15 years, considering that not all methods accounted for benthic cover or consumer biomass in the same way. Observations from the Coral Reef Assessment and Monitoring Program[46], which was conducted at over 40 fixed sites across the MHI, and diver survey data from NOAA's Coral Reef Ecosystem Division (CRED) both utilized visual estimation procedures that required benthic cover state-variables to sum to 100%. Because CORSET does not allow the paramerization of open space, cyanobacteria nor 'other' living benthos, and the four modeled state variables must sum to 100%, we re-categorized and normalized empirical data to match CORSET's requirements.

Sensitivity Analysis

Using our spatially-explicit, regional-scale biophysical model, we investigated several aspects of model sensitivity and behavior. The first two exercises, in identifying high leverage parameters and their effects on recovery trajectories, is a replication of the preliminary analyses performed by [6] to investigate whether the MHI system behaved similarly to previous instantiations. We used reef community composition, visualized in multivariate space, as the response variable to forcing parameters. Principal Components Ordination (PCA) was performed using the vegan[47] package in the R statistical program[48].

IDENTIFYING HIGH-LEVERAGE PARAMETERS

We first investigated which parameters are higher-leverage by running three 100-year simulations, with each parameter fixed at either its plausible maximum or minimum initial values, with all other parameters allowed to vary randomly within their range. For parameters that did not have a range, we fixed values at ±10% of their given value[23,27]. Under a 'null' case, all parameters were allowed to vary randomly within their ranges. We present the terminal reef state using normalized reef state data in principal ordination space. This approach allows for the full range of potential behaviors to be investigated, and replicates the default model behavior; however, synergistic effects of parameters on system dynamics cannot be quantified by this method.

INDUCED BLEACHING

To provide direct comparison between published results and this instantiation, we also simulated a high-mortality (60%) bleaching event across all subregions in year 2055 to evaluate the recovery capacity of the modeled system. We fixed the 10 highest-leverage parameters from the preceding analysis at each of their minimum and maximum values, with the supposition that these influential parameters may be similarly crucial in disturbance regimes. If shown to be the case, this approach justifies the direct manipulation of "high leverage" parameters in future, management-driven scenario tests.

SPATIAL AND TEMPORAL SENSITIVITY

The MHI instantiation of CORSET uses a gridded basemap with cell dimensions equal to 2km x 2km. Because local dynamics are coupled spatially via larval connectivity, the number of "occupied" reef cells – potential source/sink larval nodes – changes in tandem with basemap resolution. Therefore, [6] compared model behavior at resolutions of $0.5km^2$, $1km^2$, $2km^2$ for the Meso-American Region, the same magnitude of difference as the Main Hawaiian Islands (1km x 1km, 2km x 2km, and 4km x 4km). That study found were no ecologically significant differences found between spatial resolutions of the same magnitude difference as our instantiation ($0.5km^2$, $1km^2$, $2km^2$ for the Meso-American Region).

The CORSET model updates using a discrete time step. While output is reported on a yearly basis, this updating interval is the rate at which ecological dynamics take place within the model. A small interval therefore approximates continuous models[41,49]. This is mathematically advantageous as it requires fewer restraints to keep steady-state variables within a realistic domain, though it can exponentially increase computational demand for model processing. For this analysis, in replication of [6], we compared model behavior under daily, weekly, fortnightly, monthly and yearly updating intervals. Models conducted under yearly and monthly updating intervals exited the biological domain (tending towards +infinity) in 100% of runs. Smaller intervals (daily, weekly, fortnightly) remained within the domain. Such behavior suggests there exists a tolerance threshold within the updating interval; overall trends in community composition at steady state were similar among the three smaller intervals.

RESULTS

MODEL INSTANTIATION

The completed model instantiation includes basemaps and larval connectivity matrices at each of 1km, 2km, and 4km cell-side resolutions. The domain was represented in three resolutions: 1km x 1 km, 2 km x 2 km, and 4 km x 4 km. The 2 km x 2 km resolution (Figure 3B) was used for the all validation and simulation procedures.

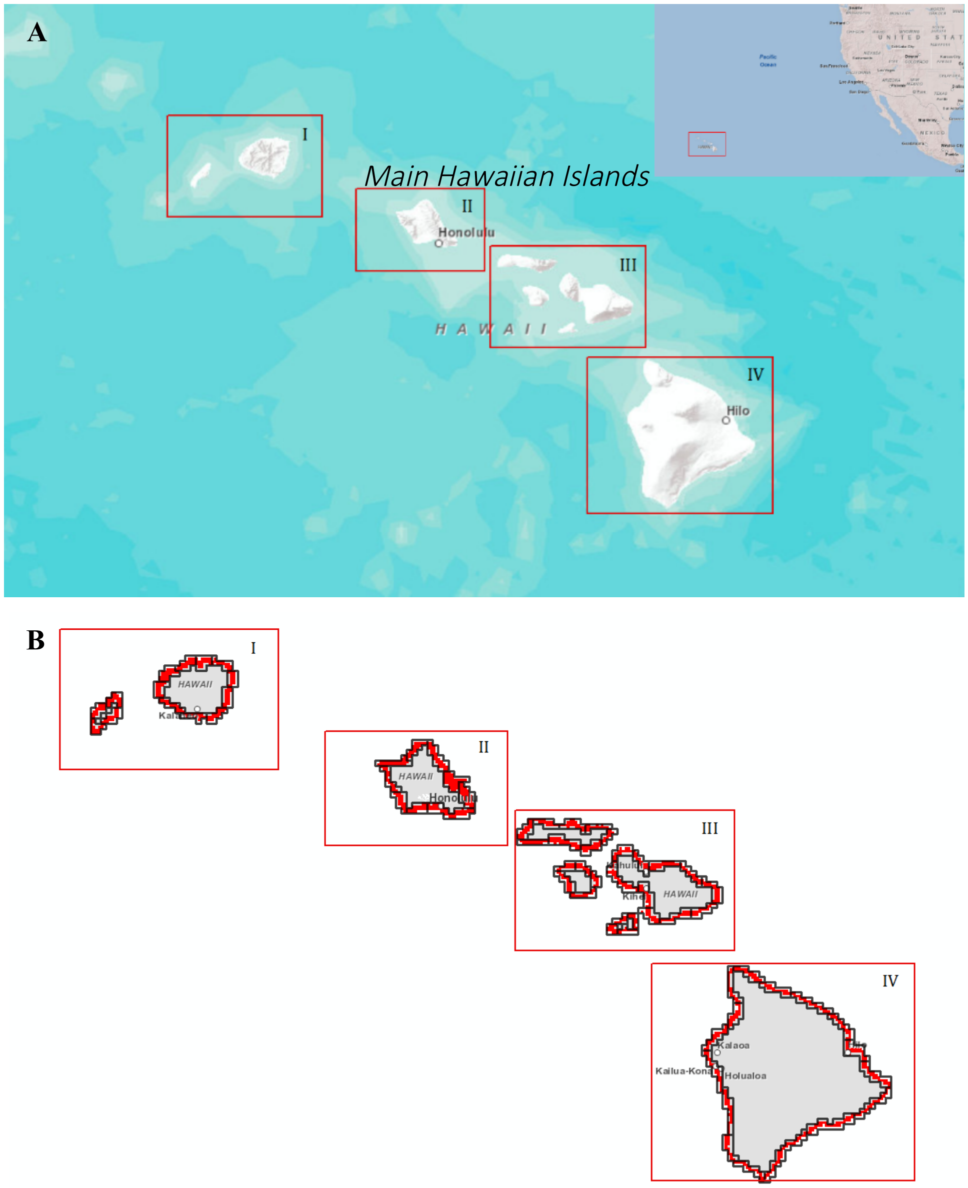
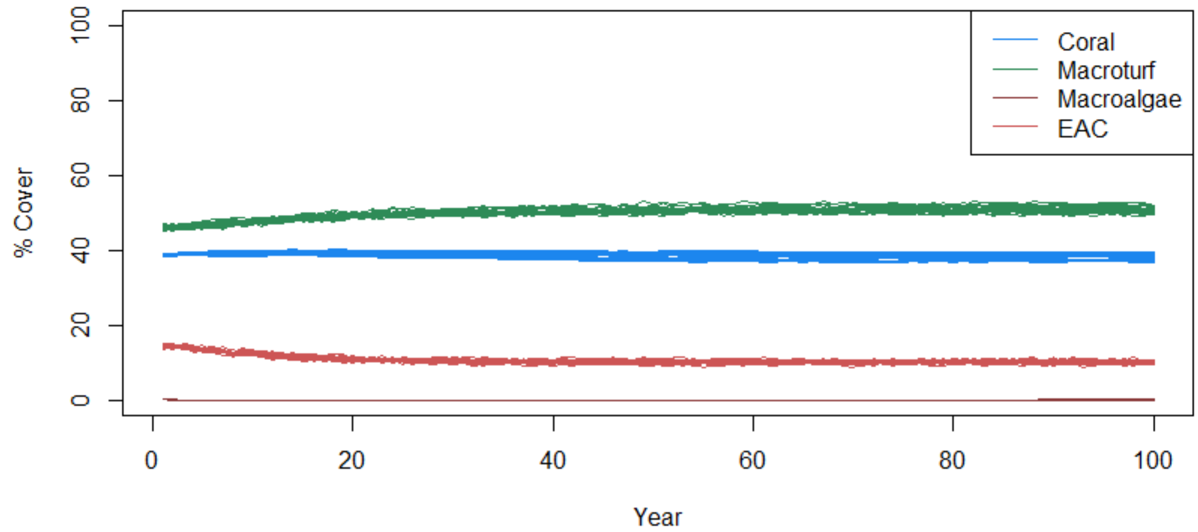


FIGURE 2A,B. VISUALIZATION OF BASEMAP CONSTRUCTED FOR THE MHI INSTANTIATION OF CORSET. A) MAIN HAWAIIAN ISLANDS, THE MODEL DOMAIN, WITH FOUR SUBREGIONS INDICATED IN RED BOXES: I: KAUAI-NI'IHAU II: O'AHU III: MAUI NUI (ISLANDS OF MAUI, LANA'I, MOLOKA'I AND KAHO'OLAWE) IV: BIG ISLAND OF HAWAII. B) GRIDDED 2 KM^2 X 2 KM^2 BASEMAP; EACH CELL REPRESENTS A REEF. THICK BLACK OUTLINES DENOTE LARVAL CONNECTIVITY POLYGONS.

MODEL VALIDATION

STABLE STATE

In the absence of forcings, CORSET exhibited steady-state behavior for all variables after ~30 years (Figure 4A,B).



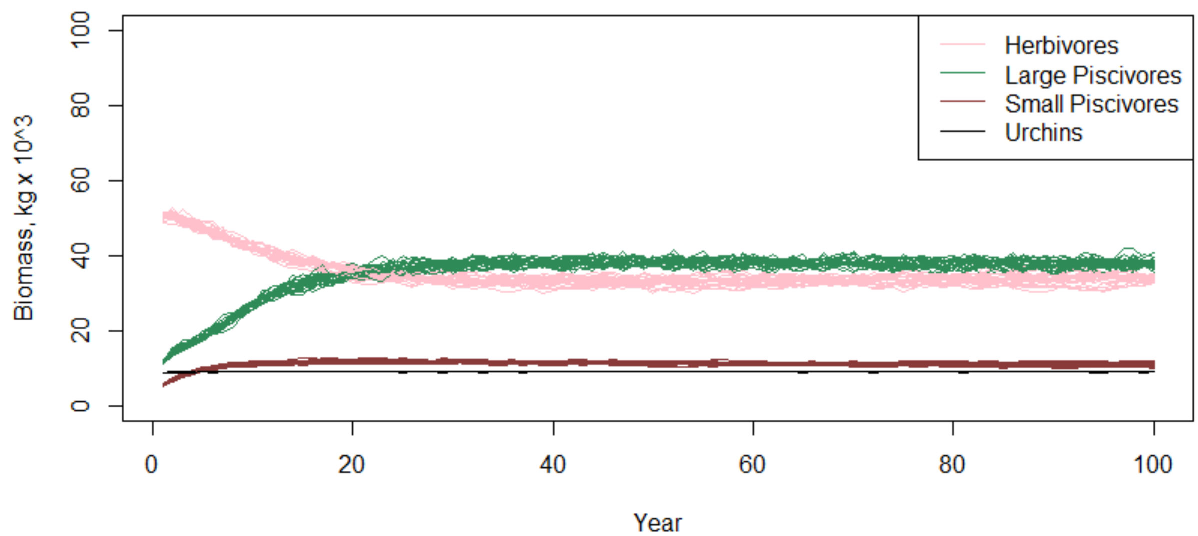


FIGURE 3A,B. MODEL TRAJECTORIES FOR BENTHIC AND CONSUMER VARIABLES, YEAR 0 – 100, FROM 25 RUNS OF 10 MONTE CARLO SIMULATIONS. WITH NO FORCINGS. CORSET DEMONSTRATES STABLE-STATE DYNAMICS AFTER ~30 YEARS. CONSUMER PARAMETERS (B) REACH STABLE STATE AT A QUICKER RATE (~ 20 YEARS) THAN BENTHIC PARAMETERS (A). THERE IS MORE VARIABILITY IN END-STATE VALUES FOR CONSUMER THAN FOR BENTHIC VARIABLES.

MODEL ACCURACY

To test whether the model could accurately reproduce observed values for current community composition, we simulated real-world coral bleaching events at years 1996, 2002 and

2014, with proportional damage ranging between 0.05 and 0.15%. Additionally, best estimates for historical and current fishing pressure were incorporated into model runs as a linear increase in fishing pressure across all functional groups. CORSET produced values for coral and macroalgal cover with reasonable correspondence to observed values; see discussion for interpretation of spatial accuracy. Modeled macroturf cover was correctly consistently higher than coral. CORSET accurately captured the wide discrepancy between macroturf and coral cover in Oahu and the Big Island of Hawai'i. Model outputs demonstrate reasonable correspondence with empirically observed points[32,46] for benthic cover (where available) at the regional scale, with variation in accuracy from small to large modeled area at the subregional scale. CORSET captured the mild decline in coral cover and corresponding increase in algal cover following three coral bleaching events, in 1996, 2002 and 2014.

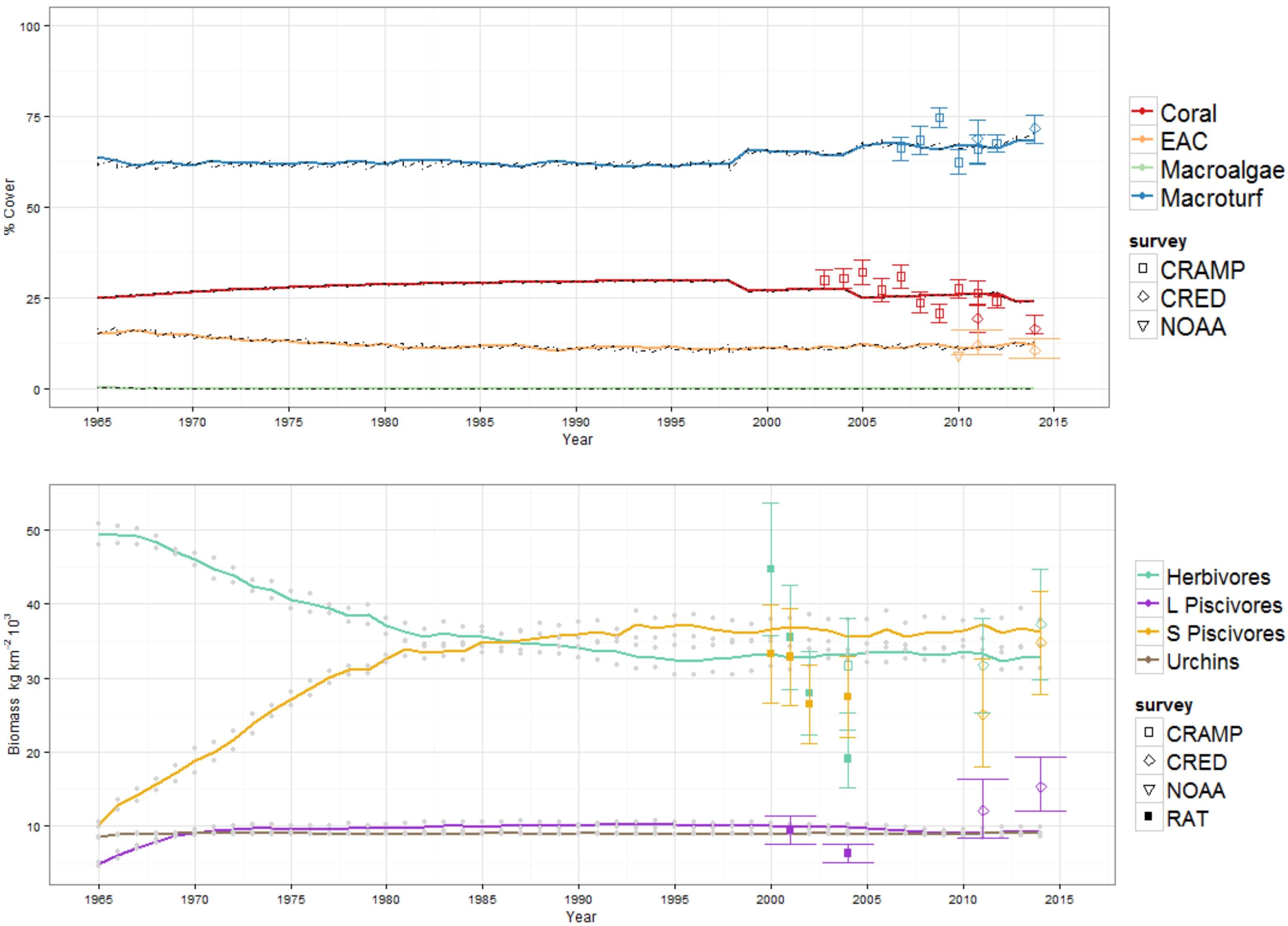


FIGURE 4A,B. REGIONAL AVERAGE BENTHIC (A) AND CONSUMER (B) PARAMETER TRAJECTORIES FOR MODEL VALIDATION, YEARS 1965 – 2015, FROM 10 MONTE CARLO SIMULATIONS. DASHED LINES REPRESENT 95% CONFIDENCE INTERVALS FOR EACH YEAR.

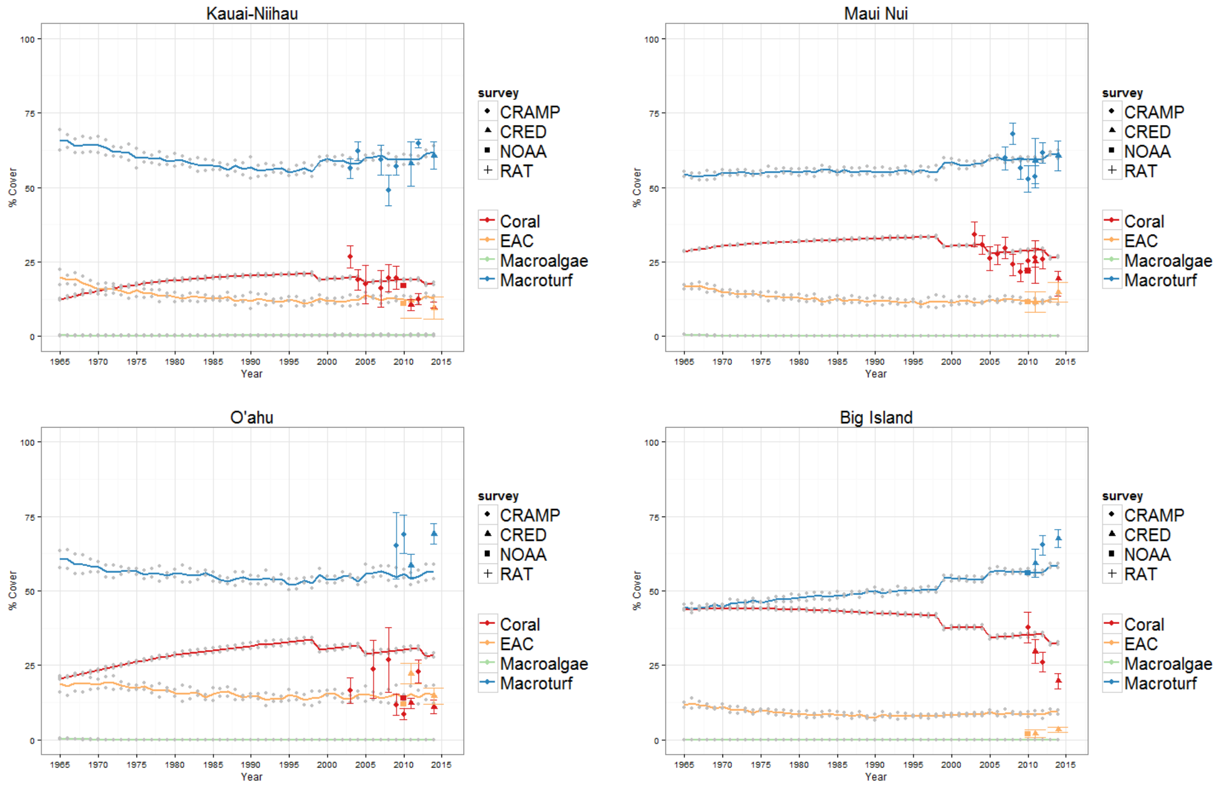


Figure 5. Subregional model trajectories for benthic parameters from 1965 to present from 10 Monte Carlo runs. Dashed lines represent 95% confidence intervals for each year.

CONSUMER STATE VARIABLES, MODEL ACCURACY

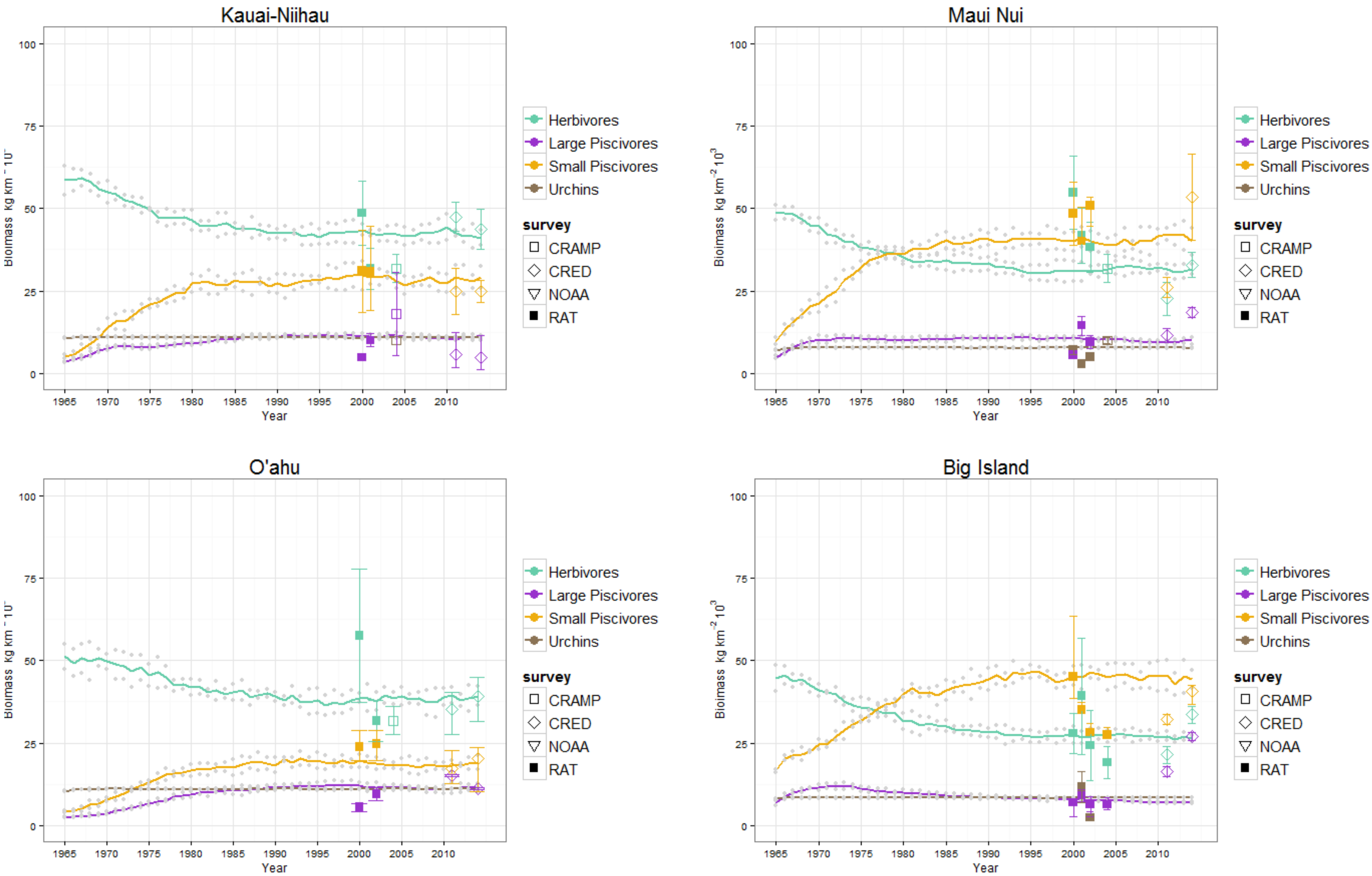


FIGURE 6. SUBREGIONAL MODEL TRAJECTORIES FOR CONSUMER PARAMETERS FROM 1965 TO PRESENT FROM 10 MONTE CARLO RUNS. DASHED LINES REPRESENT 95% CONFIDENCE INTERVALS FOR EACH YEAR.

SENSITIVITY ANALYSIS

HIGH LEVERAGE PARAMETERS

Results from the parameter sensitivity analysis, in which every parameters was fixed at either its maximum or minimum value and averaged across three 100-year runs, are displayed in Figures 7 - 9.