Canadian Journal of Fisheries and Aquatic Sciences
Journal canadien des sciences halieutiques et aquatiques

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Journal:	<i>Canadian Journal of Fisheries and Aquatic Sciences</i>
Manuscript ID	cjfas-2016-0200.R1
Manuscript Type:	Article
Date Submitted by the Author:	03-Nov-2016
Complete List of Authors:	Kapur, Maia; University of Hawai'i at Manoa, Hawaii Institute of Marine Biology Franklin, Erik; University of Hawai'i at Manoa, School of Ocean and Earth Science and Technology
Keyword:	MODELS < General, CORAL REEFS < Environment/Habitat, MARINE FISHERIES < General, MARINE PROTECTED AREAS < Environment/Habitat, LAND USE < General

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Simulating future climate impacts on tropical fisheries: are contemporary spatial fishery management strategies sufficient?

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Abstract

We demonstrated a possible future wherein coral reefs shift to an algae-dominated state that retains low coral cover and a functional biomass of herbivorous fishes that sustains a reef fish fishery. We evaluate the effect of no-take MPAs and increased coastal nutrients under two IPCC climate scenarios for years 2000-2100, which are implemented as coral bleaching events. Coral mortality from bleaching events drove a lagged increase in herbivorous fish populations, via a shift from coral-dominated to algae-dominated habitats. Biomass and catch of piscivorous fish declined significantly with the fishery shifting to the harvest of herbivorous fish. No-take MPAs for 20% of reef areas represented a threshold that had a positive effect on herbivorous fishes but no influence on the steep declines of corals and piscivorous fishes. Contemporary no-take MPAs protect less than 1% of coral reef areas around the Hawaiian Islands; significant management action would be required to approach the 20% area threshold.

Introduction

Coral reefs are globally in decline, with trajectories further threatened by diseases, pollution, coral bleaching, unsustainable fishing practices, and ocean acidification (Miller et al. 2009; Selig et al. 2010; De'ath et al. 2012). A major challenge to marine decision-making is deciphering the contribution of complex ecosystem dynamics to environmental outcomes across broad geographic scales. Agencies tasked with managing reef ecosystems 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” fishery management scenarios against changes in ocean chemistry, storm events and temperature. The need to evaluate fishery dynamics in complex ecosystem settings has led to the development and use of ecosystem end-to-end models for coral reef ecosystems (Ainsworth et al. 2008; J. Melbourne-Thomas et al. 2011; Weijerman et al. 2013). A predictive, decision-support model should include a broad set of ecological, and climatic factors unique to the system of interest while the incorporation of spatial dynamics addresses the potential for testing fishery management strategies amidst climate change effects (Rogers et al. 2015).

While negative anthropogenic impacts are severe in many coral reef ecosystems worldwide, the condition of Hawaiian coral reefs has been relatively stable in recent decades (Dollar & Grigg 2004; Walsh et al. 2013; Rodgers et al. 2015), with the effects of environmental factors driving broad-scale patterns in coral community structure. However, prior studies have limited their focus to impacts on a few ecosystem components (i.e., coral species), and a limited set of environmental stressors such as seawater temperature and acidification (Buddemeier et al. 2011; Hoeke et al. 2011). While the Hawaiian reef ecosystem has demonstrated recent stability at a regional scale, this does not negate the importance of examining reef dynamics to identify potential sensitivities for reef trajectories in the future decades, especially with a recent coral

bleaching event indicating a possible imminent increase in climate-related effects on Hawaiian reefs (Bahr et al. 2015).

Three prominent threats to Hawaiian coral reefs are coral bleaching (Hoegh-Guldberg 1999; Rodgers et al. 2010), nutrients and pollutants from terrestrial sources (Layman et al. 2011; Most 2012), and unsustainable fishing practices (Friedlander et al. 2007). The effects of climate change are expected to increase the prevalence and intensity of degree-heating weeks (DHW), which describe a time period when sea surface temperatures persistently exceed a temperature threshold that can lead to coral mortality from bleaching (Van Hooidek et al. 2014). The decline of coral populations can lead to a shift to an algal-dominated benthic environment (McManus & Polsenberg 2004; Ainsworth & Mumby 2015). While humans cannot control the frequency and intensity of bleaching events, nor completely divert terrestrial input from entering the marine environment, such impacts can theoretically be modulated by fishing activities that change top-down controls upon the affected benthos (Ware et al. 1996; Russ et al. 2015). As herbivory acts as a natural control of algal overgrowth, appropriate management of the trophic structure and grazing biomass upon a reef may curtail degradation following a bleaching event (Mumby 2006; Paddock et al. 2006). In recognition of the important role that herbivores serve on reefs, the Kahekili Herbivore Fisheries Management Area was established on Maui in 2009 to protect herbivorous fish and urchin populations (Williams et al. 2016); contemporary spatial fishery management protects under 1% of coral reef areas in no-take MPAs in the Hawaiian Islands, with approximately 10% of reef areas in partially protected MPAs (Friedlander et al. 2003; Friedlander et al. 2008). A scenario-based, decision-support tool that incorporates climate change and human activities provides an ability to test and identify effective spatial fishery management strategies for the Hawaiian region for current and potential future conditions.

This study develops, validates, and characterizes the sensitivity of a new instantiation of the Coral Reef Scenario Evaluation Tool (CORSET) to the Hawaiian Islands, a chain of eight islands in the central North Pacific Ocean. CORSET was developed as a portable framework to address biophysical processes on coral reefs across multiple spatial scales (Jessica Melbourne-Thomas et al. 2011). The tool is implemented in the open-source object-oriented Python Programming Language version 2.5 (Python Software Foundation 2011). While originally parameterized for applications on Indo-Pacific and Meso-American reefs, CORSET is readily adaptable to perform scenario testing for the Hawaiian Islands reefs.

The objectives of this study were to provide the first demonstration of the model's portability to a region outside of Meso-America and the South China Sea, and to test and evaluate several spatial management strategies for Hawaiian coral reef fish fisheries with reefs experiencing coral bleaching and elevated nutrient inputs under future climate scenarios.

Methods

CORSET Structure

The CORSET model was comprised of four components: local ecology, larval connectivity, and anthropogenic and environmental forcings (Fig. 1). CORSET used a 'functional group' approach to model interactions between benthic functional groups that include two types of corals (brooding and broadcast spawning species) and three types of algae (macroalgae, turf algae, and crustose coralline algae) and consumer functional groups that include herbivorous fish, small-to-intermediate ($< 60\text{cm}$) piscivorous and large ($\geq 60\text{cm}$) piscivorous fish and sea urchins. Turf algae, which is termed 'macroturf' in CORSET's original documentation, refers to algal turfs with height greater than 2-4mm. Parameters that describe

local-scale ecological processes were selected at random from predefined, uniform ranges derived from empirical observations. The local-scale ecological model used in CORSET was a mean-field model that describes average interactions between benthic and consumer functional groups, which were coupled across subregions by larval dispersal determined from static connectivity matrices. This structure rendered CORSET as stochastic, with the inclusion of natural disturbances such as bleaching events and direct human impacts (nutrification and fishing). The model includes the possibility of additional forcing functions but we limited the disturbances in this study to bleaching events, nutrification, and fishing. A summary of implementations for human, environmental and physical forcings is found in Table S1.

Model Development and Validation

We developed a gridded basemap (Fig. 2A,B) consisting of four subregions: 1) Kauai and Niihau; 2) Oahu, 3) Maui Nui (i.e., the islands of Molokai, Lanai, Maui, and Kahoolawe), and 4) Hawaii, also known as the Big Island. The spatial extent of the study domain was 3,263,632 km² with a total reef area of 1,342 km² for reefs from 0-30 m depth. Geographically-designated subregions are ideal for organizing management efforts; there is additional genetic evidence that suggests these regions represent shared genetic population breaks (Eble et al. 2011; Toonen et al. 2011). The domain was represented in two resolutions: 2km x 2 km, and 4 km x 4 km. The 4 km x 4 km resolution was used for the all validation and sensitivity procedures. A detailed exploration of equilibrium behavior and parameter sensitivities for both the local-scale, differential (continuous) system from which CORSET was derived, and the discrete-time equation array that constitutes the model used here, are each available in the Appendix.

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.

To test whether the model could accurately reproduce observed values for current community composition when provided real world events, we used a range of proportional mortality values from historical bleaching events within the Main Hawaiian Islands (i.e, 5-15%) with the percentage indicating the proportional loss of coral cover attributable to a bleaching event alone (Hoeke et al. 2011; De'ath et al. 2012; Osborne et al. 2011). We validated the model using real-world bleaching events from the last five decades using this mortality range, which affected the entire MHI in 1996, 2014, and 2015.

Best estimates for historical and current fishing pressure were incorporated into model runs 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 ($\text{kg km}^{-2} \text{yr}^{-1}$) was calculated for each subregion (see Appendix). Historical commercial and recreational catch was estimated from prior reports (Pooley 1993). For future scenarios, we modeled fishing pressure as a direct decrease in fish biomass, apportioned between herbivorous, small-to-intermediate and large piscivorous fish groups which updated at each annual interval independently within each reef cell. Fishing pressure values were randomly selected from a uniform distribution of range 0 – 5000 $\text{kg/km}^2/\text{yr}$. In all sensitivity analyses, fishing pressure was assigned a value of zero throughout the model run. Methods and results for the sensitivity analysis can be found in the Supplementary Material.

Scenario Sweep

Table S4 depicts the complement of forcing options selected to test the interaction between spatial fishing closures of different proportions, the frequency and intensity of coral bleaching events, and simulated nutrification events constructed to test potential reef futures under various conditions.

Simulated no-take MPAs

We used a random number generator to select 5%, 10%, and 20% of coastal reef cells that were modeled as no-take MPAs; reef cells designated as no-take MPAs are excluded from fishing take. While non-contiguous no-take MPA designation is less realistic as a management strategy, CORSET does not model ‘spillover’ effects between adjacent cells, which would justify testing the effect of various aggregations of no-take regions. Furthermore, the model grid resolution is quite large (2km x 2km or 4km x 4km) compared to the extent of actual no-take MPAs so a single reef cell may adequately represent the extent of most no-take MPAs. We executed the no-take MPA simulation for both RCP 4.5 (Fig. S7) and 8.5 (Fig 4); RCP 8.5 with 0% MPAs was the baseline strategy used for comparison against all other scenarios throughout this study.

Simulated Bleaching Events

To model changes in the frequency and intensity of coral bleaching, we evaluated a suite of management strategies in the context of two Representative Concentration Pathways (RCPs): 4.5 and 8.5 (van Vuuren et al. 2011). The former represents a mitigation regime, wherein carbon emissions result in a mean global temperature increase of 1.4°C. The latter represents a high emissions regime; it is a so-called baseline scenario in that it does not include any specific climate mitigation target (Riahi et al. 2011). Using the coral bleaching visualization tool for

Google Earth (Van Hooidonk et al. 2014), we have identified spatial and temporal projections of where degree-heating weeks (DHWs) exceed 8 per annum. We interpret such an event as a “bleaching event”, e.g. under RCP 4.5, it is projected that the MHI will experience, on average, two DHW>8 events per decade through the year 2056, after which it will undergo DHW>8 annually. Under RCP 8.5, bleaching occurs with a long-term frequency of twice per decade until year 2046, after which it occurs annually; in all cases, mortality ranges from 0.05 – 0.15.

Simulated nutrification

Nutrification was modeled during the scenario sweep in a similar manner to fishing closures; At each of 5%, 10%, and 20% proportion of reef cells were designated as “affected by nutrification”. This designation converts the range of scaling factors for turf algae growth rate to 2 – 7 and coral larval production to 0.75 – 1.0. We examined RCP 8.5 scenarios wherein nutrification was forced alone and alongside the presence, in equal proportion, of MPA closures. In these cases, cells were selected at random.

Results

Model Validation

In the absence of forcings, CORSET exhibited steady-state behavior for all variables after ~30 years (Fig. 3). Compared to historical values for benthic and consumer groups and fishing pressure, the CORSET outputs demonstrated reasonable correspondence with empirically observed points (Rodgers et al. 2010; Coyne et al. 2003) for benthic cover at the regional scale. Turf algae cover was modeled consistently higher than coral. CORSET accurately captured the wide discrepancy between turf algae and coral cover in Oahu and the Big Island of Hawai’i. The model output also indicated the mild decline in coral cover and corresponding increase in algal

cover following three coral bleaching events, in 1996, 2002 and 2014, though not to as extreme a degree as suggested by empirical data (Figs. 3, S5).

Scenario Sweep

Figures 4 – 6 and Tables 1, S4 and S5 indicate results for the Scenario Sweep outlined in Table S4.

Scenario Sweep: RCP 4.5 vs. RCP 8.5

In both climate scenarios, piscivore fisheries collapsed along with the coral community at large; this occurs to a lesser degree and later in RCP 4.5.

Scenario Sweep: RCP 8.5 + no-take MPAs

Coral cover was severely reduced under all examined no-take MPA scenarios. Fishing pressure led to declines in piscivore populations even for with 20% of reef areas within no-take MPAs.

Scenario Sweep: RCP 8.5 + Nutrification

Decreases occurred in coral cover and piscivore biomass with related increases in turf algae cover, herbivore biomass, and macroalgae cover across the four time intervals (Fig. 5, Table S5).

Scenario Sweep: RCP 8.5 + no-take MPAs + Nutrification

Under increased nutrification, higher reef areas in no-take MPAs did not result in higher coral cover, as the decrease in coral larval production and increase in turf algae growth within four times more reef cells (e.g., from 5% to 20% of total cell area) overwhelms any top-down control on turf algae growth otherwise provided by a higher herbivore biomass (in high-MPA scenarios). During coral declines, fishery catch remained fairly stable but the catch composition shifted from a mix of piscivorous fishes and herbivorous fishes to predominantly herbivorous fishes (Fig. 7).

Discussion

While reef ecosystems can be difficult to capture using models, they are crucial to coastal communities and significantly threatened by a myriad of human and environmental processes. The CORSET model is a regional-scale biophysical model of coral reef ecosystems useful for testing future climate and management scenarios in the Main Hawaiian Islands. This instantiation of the CORSET model to the MHI demonstrated its ability to simulate real-world outcomes and respond reasonably to high-disturbance regimes. Since the model was originally developed as a decision support tool, we simulated a suite of management scenarios under projected coral bleaching regimes to explore the effect of various marine protected area sizes and nutrification loads on reef community state variable trajectories.

Hawaiian corals at the 100-year time horizon decline significantly in every scenario examined, including those with 20% fishery closures. However, these results do not suggest collapse of the entire reef community. The prevailing paradigm, that reducing fishing pressure will mitigate or even reverse a coral-algal phase shift, has been supported almost exclusively by work in the Caribbean and within one-time-point studies alone (Russ et al. 2015; Hughes et al. 2007; Bellwood et al. 2004; Mumby et al. 2006). A challenge to the ubiquity of the herbivore-coral relationship was recently addressed in Russ et al. (2015) wherein the relative simplicity of bottom-up regulation of fish populations by the benthos was posited as more likely and more strongly supported by long-term evidence in the Indo-Pacific than the more indirect and complex top-down hypothesis. Our study predicts region-wide decreases in coral cover yet a maintenance of herbivore biomass from increased algal populations. The reef fish fishery maintains a relatively stable trend catch by shifting the catch composition from a mix of piscivores and herbivores to predominately herbivorous fish by end of century (Fig. 7).

Elementary effects analyses of nutrification and sedimentation for the complex integrated model from which CORSET originated (Fung 2009) indicate that nutrification exhibits a range of effects upon parameter outcomes; the largest being a positive upon turf algae growth. Its effects upon coral cover are negative but only moderately so (Fung 2009). In addition, multivariate evaluations of reef predictability indicate that, taken alone, forcings that remove fish biomass decrease the predictability of reef futures, whereas forcings that target coral cover (e.g. bleaching) create a small increase in predictability. Melbourne-Thomas et al. (2010) indicated that lower variability between model runs occurs under high coral loss, reflecting that degraded reefs converge on a community composition where algal cover is high, and where coral cover and the biomass of all fish groups is low. In our example, it follows that all outcomes reached stability at decreased or marginal coral cover and fishery biomass. In the nutrification sweep, we observed a decline in confidence for scenarios that introduced high levels of nutrients and stimulated turf algae growth, which competes with macroalgae for benthic space. This sweep retained the status quo for fishing, so that these scenarios were subject to forcings that both target fish biomass and complicate mid-level ecosystem processes (competition of algae), which may explain the decrease in predictability for later years in these simulations.

Most Hawaiian reefs are a thin veneer of reef-accreted calcium carbonate upon volcanic basalt bedrock (Grigg 1998). The basalt bedrock provides a complex reef geomorphology that will remain after corals decline and provide a benthic substrate for algal populations. We suggest that Nihoa Island and Gardner Pinnacle in the Northwestern Hawaiian Islands as two present-day reference points for the future of Hawaiian reefs described by our model results. These two areas are older islands that have eroded considerably but are surrounded by predominantly basalt rock bottom that has very low coral cover, high algal cover and high herbivore biomass

approximately 300-400% greater than reefs in the main Hawaiian Islands (Friedlander & DeMartini 2002). While the loss of corals and associated fine-scale reef structure will lead to an overall diminished fish biomass, the impacts should differentially affect particular fish groups. Our results suggest that herbivorous fishes in the Hawaiian Islands, especially around volcanic high islands, are ecological “winners” under climate change.

There is inherent uncertainty regarding the spatial variability of ecological parameters. The most considerable sources of uncertainty in this model are summarized in Table 2. The model disregards seasonality entirely in terms of growth and recruitment. Finally, the model’s structure and function itself is rooted in the assumption that the functional groups selected (and those disregarded) are the most appropriate; that uniform distributions of parameter values are biologically realistic; and that forcing outcomes follow a pattern.

The historical simulation of model trajectories did not capture the decline in coral cover that seems to be suggested by empirical data. Possible causes include the fact that the model does not account for coral disease, which readily takes hold in vulnerable (e.g. recently bleached) corals; it is also possible that the recruitment or growth parameters for living corals is higher than reality. CORSET restricts benthic cover to consist of either corals, turf algae, macroalgae, or epilithic algal communities, and does not account for other substrates as are recorded in surveys throughout the region. Accordingly, the model ‘responds’ to a loss of coral cover with the overgrowth of turfs and other algae, which may result in an exaggerated value as this total is required to sum to 100%. In reality, dead coral typically yields to combination of algae, invertebrates, sand, rubble, and open space, the ignorance of which may make the difference between a persistent fish community (grazing an abundance of algae) and the successional collapse of higher trophic groups. Taken together, these warnings are meant to prevent marine

managers from assuming that a loss in coral cover is irrelevant to the wellbeing of fisheries or coastal ecosystems.

We did not explore the effect of different bleaching regimes, since it is unlikely that regional managers would be able to control the biogeochemical and climactic factors that collude on a global scale to produce thermal anomalies leading to bleaching. However, a straightforward comparison between two IPCC Representative Concentration Pathway scenarios (RCPs) indicated that, while an emissions mitigation scenario (RCP 4.5) delays the diminishment of coral cover by a decade at least, both regimes involve bleaching events too frequent to sustain current benthic community compositions and result in a regional regime shift to an algal-dominated state.

Another source of uncertainty for this model is the ability of the larval connectivity matrix approach to reflect true connectivity and recruitment processes between reef sites. While previously applied in multiple studies and informed by biophysical data for other locations (Pineda et al. 2007; Largier 2003), the connectivity matrices describe dynamics at a coarse spatial scale for the Hawaiian model and have only been validated with indirect observational data such as genetic approaches (Toonen et al. 2011). There is likely a stochastic element to larval connectivity dynamics in nearshore systems, whereas CORSET's model is based on persistent linkages between reefs over the study period.

These results should be interpreted with caution as there are ecological processes either overlooked or oversimplified within the CORSET model that may influence the viability of Hawaiian reefs under these low-cover paradigms. The model lacks any index or scaling factor for the value of benthic structure or rugosity over time. Dead and dying corals subside in tandem with turf algae overgrowth, at a rate which can only be expected to increase with higher ocean

acidification (Pratchett et al. 2009; Edinger et al. 2000). Because complex coral structure is certainly tied to the recruitment and early life histories of reef fish, it is unreasonable to expect a scenario with 2% coral cover to support the same rate of fish survival as one with ten times that amount. It is possible that mass bleaching events may not lead to immediate structural loss, which highlights the concern that CORSET does *not* accommodate the ecosystem processes provided by living vs. dead or dying corals. While fish are able to persist (e.g. spawn and hide from predators) among dead coral skeletons, calcifying algae may not produce the same rugosity, and the collapse of higher trophic groups gives way to bio-eroders that would accelerate the loss of coral structure. A possible long-term strategy would be to restrain fishing below the level at which algae out-compete corals (McClanahan 1995), though considering the predicted annual frequency of chronic bleaching events, this seems somewhat futile. In our view, it is more realistic to recalibrate the targets and benchmarks of a sustainable fishery among low trophic groups. Considering it is much more difficult to manage the many factors (pollution, erosion, acidification) that modify the benthos than to impose a no-take MPA, the suggestion that the no-take MPAs cannot guarantee a preservation of coral cover may complicate management priorities. It may require a reformulation of the target of conservation practices, with the acknowledgement that a great decline in coral cover is generally inevitable. No scenarios resulted in the persistence of higher trophic groups, suggesting that the amount of fishing pressure modeled was simply too high to sustain any semblance of current populations in the long-term future.

To summarize, we modeled a possible future wherein coral reefs shift to an algae-dominated state that retains low coral cover and a functional biomass of herbivorous fishes that sustains a reef fish fishery. We explored the effects of no-take MPAs and increased coastal

nutrients on coral reef benthic and consumer functional groups for Hawaiian coral reefs experiencing fishing and coral bleaching using the CORSET model under IPCC climate scenarios RCP 4.5 and RCP 8.5 for the years 2000-2100. Coral mortality from bleaching events drove a lagged increase in herbivorous fish populations as a shift from coral-dominated to algae-dominated habitats provided increased prey. Biomass and catch of piscivorous fish declined significantly with the fishery shifting to the harvest of herbivorous fish. No-take MPAs for 20% of reef areas represented a threshold that had a positive effect on herbivorous fishes but no influence on the steep declines of corals and piscivorous fishes. These results contradict the usual management paradigm, which emphasizes top-down ecosystem control (Mumby et al. 2006; Mumby et al. 2014; Brown & Mumby 2014; Douvre 2008), and present a new challenge in discerning the most effective means of ecosystem management for all ecological components of coral reefs.

Acknowledgements

We thank J. Melbourne-Thomas for sharing the software code for CORSET, M. Donahue and C. Mora for suggestions in study design and analysis, M. Belcaid for providing code and computing resources for the sensitivity analyses, E. Treml for his contributions on larval connectivity in Hawaii, Z. Oyafuso for model parameter values mined from the literature, and two anonymous referees whose reviews contributed to the improvement of this manuscript. This work was supported by funding from the USGS Pacific Islands Climate Science Center (G13AC00395 to ECF) and NOAA Fisheries Pacific Islands Fisheries Science Center (NA10NMF4520163 to ECF). This is SOEST contribution #9849 and HIMB contribution #1669.

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Parameter	Low no-take MPA (5%)	High no-take MPA (20%)
Coral cover (%)	Decreases coincident to bleaching events	Decreases coincident to bleaching events at slowest rate
Turf algae cover (%)	Increases over time; consistently higher than scenarios with greater protection	Increases over time; consistently lower than scenarios with less protection
Herbivorous Biomass (kg/km2)	Generally stable over time	Generally stable over time
Piscivorous Biomass (kg/km2)	Collapses after 2050; consistently lower than more-protected scenarios	Nearly collapses after 2050; barely higher than scenarios with less protection

488

489 Table 1. Summary of state variable responses to varied marine protected area regimes
490 within scenario sweep.

Category	Description	Suggestions
Larval Connectivity	Difficult to validate connectivity data derived from larval dispersal simulations	Explore dispersal simulation sensitivities to biological parameters; capture temporal stochasticity
Parameter Uncertainty	Spatial, temporal variability uncertain; uncertainty in production parameters	Identify optimal set of functional groups
Simplification of ecological dynamics	Use of uniform distribution for parameter selection; lack of temporal and spatial variability; broad assumptions about fishing pressure (e.g., linear increases)	Accommodate seasonality based on empirical data

491 Table 2. Summary of CORSET Model Limitations

Figure 1. Schematic of structure and function in CORSET. Mean-field equations describing local-scale interactions between benthic and consumer functional groups 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. Map created using ArcGIS® software by Esri, www.esri.com.

500

501 Figure 2A,B. Visualization of basemap constructed for the MHI instantiation of CORSET.

502 A) Main Hawaiian Islands, the model domain, with four subregions indicated in red boxes:

503 I: Kauai-Ni'ihau II: O'ahu III: Maui Nui (islands of Maui, Lana'i, Moloka'i and

504 Kaho'olawe) IV: Big Island of Hawaii. B) Gridded 4 km2 x 4 km2 basemap; each cell

represents a reef. Thick black outlines denote larval connectivity polygons. Map created using ArcGIS® software by Esri, www.esri.com.

Figure 3. Regional model trajectories for consumer (upper) and benthic (lower) parameters from 1965 to present from 100 Monte Carlo runs. Grey points represent 95% confidence intervals for each year.

512

513 Figure 4. Modeled state variable responses for four no-take MPA scenarios under RCP 8.5.

514 Each panel represents a single response variable; individual boxes are color-coded by the

515 percentage of reef cells closed to fishing activity.

Figure 5. Modeled state variable responses for four nutrification regimes under RCP 8.5. Each panel represents a single response variable; individual boxes are color-coded by the percentage of reef cells affected by nutrification.

Figure 6. Modeled state variable responses for four paired no-take MPA + nutrification regimes under RCP 8.5. Each panel represents a single response variable; individual boxes are color-coded by the percentage of reef cells affected by nutrification and closed to fishing activity.

Figure 7. Fishery catch of herbivorous fishes and piscivorous fishes for no-take MPA +
 nutrification regimes under RCP 8.5. Each panel represents a single response variable; individual
 boxes are color-coded by the percentage of reef cells affected by nutrification and closed to
 fishing activity.

1 Local Scale Ecological Model.

2 Please refer to the following for a detailed exploration of equilibrium behavior and parameter

3 sensitivities for both the local-scale, differential (continuous) system from which CORSET was

4 derived, and the discrete-time equation array that constitutes the model used here:

5 Jessica Melbourne-Thomas, Craig R. Johnson, Tak Fung, Robert M. Seymour, Laurent M.

6 Chérubin, J. Ernesto Arias-González, and Elizabeth A. Fulton. 2011. Regional-scale scenario

7 modeling for coral reefs: a decision support tool to inform management of a complex

8 system. *Ecological Applications* 21:1380–1398. The local-scale ecological model (Ecological

9 Archives A021-064-A).

10 **Table A1.** Local model parameter definitions and values derived for the Main Hawaiian Islands.

11 Parameter values are derived using the same parameterization methodology as detailed in Fung

12 (2009). Mathematically derived parameter restrictions detailed in the footnotes are required to

13 keep state variables within a realistic biological range, i.e. in the range 0–1 for benthic covers,

14 and ≥ 0 (but not tending to infinity) for consumer biomasses (see Fung, 2009, for detailed

15 derivations).

Benthic Parameters

d_C	The background mortality rate of brooding and spawning corals	0.02–0.1 yr ⁻¹ (Bythell, Gladfelter, & Bythell, 1993; Lirman, 2003; Nugues & Bak, 2006)
r_C	The growth rate of existing coral over grazed EAC	0.04–0.2 yr ⁻¹ (Babcock, 1985; Chornesky & Peters, 1987; Edmunds, 2007; Huston, 1985; Koop et al., 2001; Langmead & Sheppard, 2004; Sandin et al., 2008)
a_C	The growth rate of coral over macro turf, relative to its growth over grazed EAC	0 – 1
ε_C	The recruitment rate of coral onto macro turf, relative to the rate onto grazed EAC	0.05–0.15 (Birrell et al., 2005)
ξ_{Cb}, ξ_{Cs}^a	The recruitment rates of brooding and spawning corals onto grazed EAC	Modeled separately

g_T	The maximum rate (per unit of grazing pressure θ) at which existing macroturf is grazed down	$5 - 15 \text{ yr}^{-1}$ (Birrell et al., 2005; Mumby & Dytham, 2006)
ζ_T	The rate at which grazed EAC grows into macroturf	$2 - 20 \text{ yr}^{-1}$ (McClanahan, Polunin, & Done, 2002; Mumby & Dytham, 2006)
g_M	The maximum rate (per unit of grazing pressure θ at which existing macroalgae is grazed down	$0.05 - 15 \text{ yr}^{-1}$ (Bellwood, Hughes, & Hoey, 2006; Hay, 1991; Hughes et al., 2007; Mumby & Dytham, 2006; G R Russ & St. John, 1988; Garry R. Russ, 2003)
r_M	The growth rate of macroalgae over grazed EAC	$0.05 - 0.4 \text{ yr}^{-1}$ (Mumby, Foster, & Fahy, 2005)
β_M	Coral growth is inhibited by the presence of nearby macroalgae and this is represented as a depression of r_C by the factor $(1 - \beta_M M)$ 27	$0.4 - 0.9 \text{ yr}^{-1}$ (Arias-González, 1998; Babcock, 1985; Chornesky & Peters, 1987; Edmunds, 2007; Garcia-Salgado & Nava-Martinez, 2008; Hay, 1984; Huston, 1985; Koop et al., 2001; Langmead & Sheppard, 2004; Sandin et al., 2008; Van Rooij, Videler, & Bruggemann, 1998)
γ_{MC}	The growth rate of macroalgae over coral, relative to its growth over grazed EAC	$0 - 0.9$ (Box & Mumby, 2007; Mumby et al., 2005; Nugues & Bak, 2006)
γ_{MT}	The growth rate of macroalgae over macroturf, relative to its growth over grazed EAC	$0 - 0.9$ (Box & Mumby, 2007; Mumby et al., 2005; Nugues & Bak, 2006)

Consumer parameters

i_H	A parameter that measures the inaccessibility of algae (turf and macroalgae) to herbivorous fish grazing	$3 \times 10^3 - 5 \times 10^5 \text{ kg/km}^2$ (Aliño et al., 1993; Arias-González, 1998; S. R. Carpenter, Kitchell, & Hodgson, 1985; Craig, Green, & Tuilagi, 2008; Friedlander & DeMartini, 2002; Garcia-Salgado & Nava-Martinez, 2008; Gardner, Côté, Gill, Grant, & Watkinson, 2005; Gribble, 2003; P. a. Kramer, 2003; Letourneur, Kulbicki, & Labrosse, 1998; Mangi & Roberts, 2007; McClanahan, Kamukuru, Muthiga, Yebio, & Obura, 1996; Newman, Paredes, Sala, & Jackson, 2006; Sandin et al., 2008; Tsehay & Nagelkerke, 2008; Van Rooij et al., 1998; Williams & Hatcher, 1983)
i_{PH}	A parameter that measures the inaccessibility of herbivorous fish to predation by piscivorous fish	$7 \times 10^3 - 1 \times 10^4 \text{ kg/km}^2$ (Aliño et al., 1993; Arias-González, 1998; S. R. Carpenter et al., 1985; Craig et al.,

		2008; Friedlander & DeMartini, 2002; Garcia-Salgado & Nava-Martinez, 2008; Gardner et al., 2005; Gribble, 2003; P. a. Kramer, 2003; Letourneur et al., 1998; Mangi & Roberts, 2007; McClanahan et al., 1996; Newman et al., 2006; Sandin et al., 2008; Tsehay & Nagelkerke, 2008; Van Rooij et al., 1998; Williams & Hatcher, 1983)
i_{FH}	A parameter that measures the inaccessibility of herbivorous fish to fishers	$7 \times 10^{-2} - 1 \times 10^3 \text{ kg/km}^2$ ^{25,31-38}
dH^b	The death rate of herbivorous fish from all factors other than predation by piscivorous fish and fishing	$0.3 - 3 \text{ yr}^{-1}$ (Froese & Pauly, 2011)
μ_M, μ_T, μ_E^c	The herbivorous fish biomass accumulated from grazing on 100% cover of macroalgae, macroturf and EAC respectively, and which contributes to somatic growth of herbivorous fish	$900 - 5 \times 10^5 \text{ kg km}^{-2} \text{ yr}^{-1}$ (Aliño et al., 1993; Arias-González & Morand, 2006; Arias-González, 1998; Bellwood, Hughes, Folke, & Nyström, 2004; Ebert, 1975; Gardner et al., 2005; Gribble, 2003; Johnson, Klumpp, Field, & Bradbury, 1995; Van Rooij et al., 1998)
ρ_H	The proportion of total fishing pressure f which acts on herbivorous fish ($\rho_H + \rho_{Ps} + \rho_I = 1$)	$0 - 1$
ξ_H^a	The recruitment rate of herbivorous fish	Modeled separately $7 \times 10^3 - 1 \times 10^4 \text{ kg/km}^2$ (Aliño et al., 1993; Arias-González, 1998; R. C. Carpenter, 1986; Craig et al., 2008; Edwards et al., 2014; Friedlander & DeMartini, 2002; Garcia-Salgado & Nava-Martinez, 2008; Gardner et al., 2005; Gribble, 2003; P. a. Kramer, 2003; Letourneur et al., 1998; Mangi & Roberts, 2007; McClanahan, 1996; Newman et al., 2006; Tsehay & Nagelkerke, 2008; Van Rooij et al., 1998; Williams & Hatcher, 1983)
i_{PIPs}	A parameter that measures the inaccessibility of small-to-intermediate piscivorous fish to predation by large piscivorous fish	$7 \times 10^2 - 1 \times 10^3 \text{ kg/km}^2$ (Aliño et al., 1993; Arias-González, 1998; R. C. Carpenter, 1986; Craig et al., 2008; Edwards et al., 2014; Friedlander & DeMartini, 2002; Garcia-Salgado & Nava-Martinez, 2008; Gardner et al., 2005; Gribble, 2003; P. a. Kramer, 2003; Letourneur et al., 1998; Mangi & Roberts, 2007; McClanahan, 1996; Newman et al., 2006; Tsehay & Nagelkerke, 2008; Van Rooij et al., 1998; Williams & Hatcher, 1983)
i_{FPs}	A parameter that measures the inaccessibility of small-to-intermediate piscivorous fish to fishermen	$7 \times 10^2 - 1 \times 10^3 \text{ kg/km}^2$ (Aliño et al., 1993; Arias-González, 1998; R. C. Carpenter, 1986; Craig et al., 2008; Edwards et al., 2014; Friedlander & DeMartini, 2002; Garcia-Salgado & Nava-Martinez, 2008; Gardner et al., 2005; Gribble, 2003; P. a. Kramer,

		2003; Letourneur et al., 1998; Mangi & Roberts, 2007; McClanahan, 1996; Newman et al., 2006; Tsehaye & Nagelkerke, 2008; Van Rooij et al., 1998; Williams & Hatcher, 1983)
d_{ps}^d	The death rate of small-to-intermediate piscivorous fish from all factors other than predation and fishing	$dP_{smin} - 2 \text{ yr}^{-1}$ (Froese & Pauly, 2011)
gP_s	The maximum predation rate of small-to-intermediate piscivorous fish on herbivorous fish	$1-2 \text{ yr}^{-1}$
ϕP_s	The proportion of small-to-intermediate piscivorous fish biomass that becomes large piscivorous fish biomass due to predation and subsequent growth	$0 - 10$
ρP_s	The proportion of total fishing pressure f which acts on small-to-intermediate piscivorous fish ($\rho_H + \rho_{ps} + \rho_{pl} = 1$)	$0 - 1$
ξP_s^a	The recruitment rate of small-to-intermediate piscivorous fish	Modeled separately $0.2 - 3 \text{ yr}^{-1}$ (Aliño et al., 1993; Arias-González, 1998; R. C. Carpenter, 1986; Craig et al., 2008; Edwards et al., 2014; Friedlander & DeMartini, 2002; Garcia-Salgado & Nava-Martinez, 2008; Gardner et al., 2005; Gribble, 2003; P. a. Kramer, 2003; Letourneur et al., 1998; Mangi & Roberts, 2007; McClanahan, 1996; Newman et al., 2006; Tsehaye & Nagelkerke, 2008; Van Rooij et al., 1998; Williams & Hatcher, 1983)
i_{FPI}	A parameter that measures the inaccessibility of large piscivorous fish to fishermen	
dP_l^e	The death rate of large piscivorous fish from all factors other than predation and fishing	$7 \times 10^2 - 1 \times 10^3 \text{ kg/km}^2$ (Froese & Pauly, 2011)
gP_l	The maximum predation rate of large piscivorous fish on herbivorous fish	$0.25-0.75 \text{ yr}^{-1}$
rP_l	The proportion of consumed biomass which is used for somatic growth, for large piscivorous fish	$0.03-0.09$
P_l	The predation rate on small-to-intermediate piscivorous fish by large piscivorous fish, relative to that on herbivorous fish	$2 - 4$
ρP_l^f	The proportion of total fishing pressure f which acts on large piscivorous fish ($\rho_H + \rho_{ps} + \rho_{pl} = 1$)	$0 - 1$
f	The maximum fishing biomass which can be caught	$0-5 \times 10^3 \text{ kg km}^{-2} \text{ yr}^{-1}$
qU^g	Quadratic mortality of urchins	$5 \times 10^7 \text{ yr}^{-1}$
dU^f	The death rate of urchins	$0.05 - 0.6 \text{ yr}^{-1}$
K_U	A parameter that measures the biomass accumulated by urchin grazing and which contributes to somatic growth relative to that for herbivorous fish grazing	$0.7 - 3$
ξU^a	The recruitment rate of urchins	Modeled separately

λ_H	A parameter that determines the competitiveness of herbivorous fish relative to urchins	0.6–1
λ_U	A parameter that determines the competitiveness of urchins relative to herbivorous fish	$1 - 3 \times 10^6 \text{ kg/km}^2$
i_U^h	A parameter that measures the inaccessibility of algae (turf and macroalgae) to urchin grazing	$2 \times 10^3 - 2 \times 10^6$
16		
17	^a Recruitment terms (l_{Cb} , l_{Cs} , l_H , l_{Ps} , l_U) are modeled externally to the local model, based on	
18	matrices defining connectivity between reef cells. Parameters used for modelling larval	
19	production and post-settlement processes are provided in Appendix D.	
20	^b $d_{Hmin} = \left\{ 0.2, \frac{\max\{0.2, \mu \times \max\{gT, \zeta T\}\}}{i_H} + 0.000001 \right\}$	
21	^c	
22	$\mu_{max} =$	
23	$\min\{100,000, \mu_{max1}\}$, where $\mu_{max1} =$	
24	$\min\left\{ \frac{i_H \times (2 - 0.000001)}{\max\{gT, \zeta T\}}, \frac{i_U \times (1 - 0.000001)}{K_U \times \max\{gT, \zeta T\}} \right\}$	
25	^d $d_{Psmin} = \max\{0.2, (1 -$	
26	$(\phi_{Ps})r_{Ps}g_{Ps}\}$	
27	^e $d_{Plmin} = r_{Pl}g_{Pl}(1 + \phi_{Pl}) + 0.000001$	
28	^f $d_{Umin} = \max\left\{ 0.3, \frac{K_U \times \mu \times \max\{gT, \zeta T\}}{i_U} + \right.$	
29	$0.000001\}$	
30	^g Quadratic mortality of sea urchins, q , is included in the regional implementation of the local	
31	ecological model to prevent uncontrolled population explosions in this functional group. This	
32	term is a proxy for consumption of sea urchins by fish and invertebrate predators (Mumby,	
33	Dahlgren, Harborne, Kappel, Micheli, Brumbaugh, Holmes, Mendes, Broad, Sanchirico, Buch,	
34	Box, et al., 2006; Randall, Schroeder, & Starck II, 1964).	
35	^h $i_{Umin} = \max\left\{ 2000, \frac{60K_U \times \max\{gT, \zeta T\}}{1 - 0.000001} \right\}$	

36 **Table A2.** Larval Production, Recruitment and Post-Settlement Parameters used in CORSET.

Recruitment Parameters	Definition	Hawai'i	Type	Source(s)	Notes
l_C *	Brooding and spawning coral larval production (at 100% cover)	$6 \times 10^9 - 9 \times 10^9 \text{ km}^{-2} \text{ yr}^{-1}$		(Harrison & Wallace, 1990; Richmond, 1988)	Calibration parameter because info are sparse, uncertain, and variable. As a result, these values will remain the same.
l_H *	Herbivorous fish larval production	$4 \times 10^3 - 1 \times 10^4 \text{ kg}^{-1} \text{ yr}^{-1}$		(Cowen, Paris, & Srinivasan, 2006; Froese & Pauly, 2011)	Calibration parameter because info are sparse, uncertain, and variable. As a result, these values will remain the same
l_Ps *	Small piscivorous fish larval production	$1 \times 10^2 - 6 \times 10^2 \text{ kg}^{-1} \text{ yr}^{-1}$		(Cowen et al., 2006; Froese & Pauly, 2011)	Calibration parameter because info are sparse, uncertain, and variable. As a result, these values will remain the same
l_Pl *	Large piscivorous fish larval production	$1 \times 10^3 - 6 \times 10^3 \text{ kg}^{-1} \text{ yr}^{-1}$		(Cowen et al., 2006; Froese & Pauly, 2011)	Calibration parameter because info are sparse, uncertain, and variable. As a result, these values will remain the same
l_U *	Urchin larval production	$2 \times 10^5 - 4 \times 10^5 \text{ kg}^{-1} \text{ yr}^{-1}$		(Leviton, 1988, 1991)	Calibration parameter because info are sparse, uncertain, and variable. As a result, these values will remain the same
dlarv_Cb	Initial mortality of brooded coral larvae	0.6 – 0.99		(Fadlallah, 1983)	QE565.C68 Vol 2 p.129 - 150
drec_C	Mortality of brooding and spawning coral recruits during the first year following settlement	$0.2 - 0.7 \text{ yr}^{-1}$	Range	(Babcock, 1985)	Assumes that brooded larvae are competent to settle within an average period of four days (Fadlallah, 1983) and that average pre-settlement mortality is between 0.2 day^{-1} and 0.7 day^{-1} (as for post-settlement mortality of coral larvae). Pre-settlement mortality is implicit in connectivity

				matrices for spawned coral, and urchin larvae.
drec_F	Mortality of fish recruits during the first year following settlement	0.2 yr ⁻¹	minimum	(Beukers & Jones, 1997; Doherty & Fowler, 1994) Lowest mortality rate reported
drec_U	Mortality of urchin recruits during the first year following settlement	0.11 - 0.32 yr ⁻¹	range	(Beukers & Jones, 1997; Doherty & Fowler, 1994) Ebert (2013), edited by Lawrence, Sea Urchins: Biology and Ecology 38
arec_C	The area of 1 yr old coral recruits	2.18 cm ²	point estimate	(Edmunds, 2007) Assumes all recruits are ~ 16.5 mm diameter or 14.7 mm on a side of a square
brec_H	The biomass of 1 yr old herbivorous recruits	80 g	point estimate	(Froese & Pauly, 2011)
brec_P	The biomass of 1 yr old piscivorous fish recruits	150 g	point estimate	(Froese & Pauly, 2011)
brec_U	The biomass of 1 yr old urchin recruits	10 g	point estimate	(R. Carpenter, 1997; Levitan, 1988)

Table A3. Fishing Pressure across the Main Hawaiian Islands, 1965 – 2015

These values are an estimated linear increase of ~24% across four subregions of the MHI, Kauai-Niihau, O’ahu, Maui Nui, and the Big Island of Hawai’i. The values indicate fishing pressure, in $\text{kg} \times 10^3 \text{ km}^{-2} \text{ yr}^{-1}$, for each (Dirk Zeller, Booth, Craig, & Pauly, 2006) of 50 years from 1965 - present. Historical commercial fishing pressure (Pooley 1993) was incorporated to a hind-cast using 1980 recreational catch estimates (Pooley 1993), scaled to the HI state population (US Census). Total catch was apportioned across subregions using present-day percent-of-total catch from Hawaii Department of Aquatic Resources commercial fisheries reporting (2003 – 2011). This per-capita interpolation method is a desirable alternative to the unsatisfactory method of assuming “zero catch” for years wherein data is absent (D Zeller, Froese, & Pauly, 2005; Dirk Zeller et al., 2006).

Fishing Area (km^2)	Subregion			
	Kaua’i – Ni’ihau 1036	O’ahu 992	Maui Nui 1868	Hawai’i 1500
Year	Fishing Pressure, $\text{kg} \times 10^3 \text{ km}^{-2} \text{ yr}^{-1}$			
1965	495	5156	699	1013
1966	498	5187	705	1023
1967	501	5219	711	1032
1968	504	5250	717	1042
1969	507	5282	723	1052
1970	510	5313	729	1062
1971	513	5345	735	1071
1972	516	5376	741	1081
1973	519	5408	747	1091
1974	522	5439	753	1101
1975	525	5471	759	1110
1976	528	5502	765	1120
1977	531	5534	771	1130
1978	534	5566	777	1140
1979	537	5597	783	1149
1980	540	5629	789	1159
1981	543	5660	795	1169
1982	546	5692	801	1179
1983	550	5723	807	1188

1984	553	5755	813	1198
1985	556	5786	819	1208
1986	559	5818	825	1218
1987	562	5849	831	1227
1988	565	5881	837	1237
1989	568	5912	843	1247
1990	571	5944	850	1257
1991	574	5975	856	1266
1992	577	6007	862	1276
1993	580	6038	868	1286
1994	583	6070	874	1295
1995	586	6101	880	1305
1996	589	6133	886	1315
1997	592	6165	892	1325
1998	595	6196	898	1334
1999	598	6228	904	1344
2000	601	6259	910	1354
2001	604	6291	916	1364
2002	607	6322	922	1373
2003	610	6354	928	1383
2004	613	6385	934	1393
2005	616	6417	940	1403
2006	619	6448	946	1412
2007	622	6480	952	1422
2008	625	6511	958	1432
2009	628	6543	964	1442
2010	631	6574	970	1451
2011	634	6606	976	1461
2012	637	6637	982	1471
2013	640	6669	988	1481
2014	643	6700	994	1490

49 Appendix Reference List

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FORCING	IMPLEMENTATION
CORAL BLEACHING	Coral bleaching events were simulated via the “coral mortality” forcing term, with the years and proportional mortalities of specific bleaching events specified by the user and occurring randomly among all subregions during each interval. Proportion of coral cover lost (i.e., due to mortality) from bleaching events were randomly selected from a uniform distribution of range 0.05 – 0.15.
FISHING PRESSURE	Modeled as a direct decrease in fish biomass, apportioned between herbivorous, small-to-intermediate (< 60cm) piscivorous and large ($\geq$ 60cm) piscivorous fish groups and updates at each annual interval independently within each reef cell. Fishing pressure values were randomly selected from a uniform distribution of range 0 – 5000 kg/km ² /yr.
LARVAL CONNECTIVITY	Reef cells interacted geographically via static larval connectivity matrices, derived from oceanographic and genetic studies; previous instantiations utilized simulative outputs from the three-dimensional Regional Ocean Modeling System (ROMS) (Shchepetkin & McWilliams 2005).
NUTRIFICATION	We modelled the effect of nutrification specifically as an increase in the scaling parameter for turf algae growth, and a depression of successful coral larval recruitment. It did not directly model impacts of increased nutrification on fish community structure or predation ability. The scaling factor for turf algae growth rate was 2 – 7; the scaling factor for coral larval production was 0.75 – 1.0. The nutrification response of algae in the regional model was based on the linear threshold model described by Bell et al. (2007). The concentration of N and P combined was assumed to be above the threshold for an algal growth response in nutrient-affected reef cells. Macroalgal growth rate in these cells was scaled by the ratio of maximum growth rate to average growth rate from published values for a range of tropical algal species (Lapointe 1989; Lapointe & O’Connell 1989; Stimson & Larned 2000; Larned 1998; Schaffelke & Klumpp 1997).

1 **Table S1.** Summary of forcing implementations used in CORSET.

2

Detailed Methods of Main Hawaiian Islands CORSET Instantiation

CORSET Structure

The CORSET 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 (macroalgae, and turf algae), herbivorous fish, small-to-intermediate sized piscivorous fish, large piscivorous fish, and sea urchins. Turf algae, which is termed ‘macroturf’ in CORSET’s original documentation, refers to algal turfs with height greater than 2-4mm. 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). A summary of forcing implementations for human, environmental and physical forcings is found in Table S1.

Model Development and Validation

We developed a gridded basemap (Figure 2A,B) 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 km² and a total reef area of 1,342 km² was modeled. Geographically-designated subregions are ideal for organizing management efforts; there is additional genetic evidence that suggests these regions represent shared genetic population breaks (Eble et al.

2011). 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 4 km x 4 km resolution was used for the all validation and sensitivity procedures. See supplemental material for details of the sensitivity analysis.

We simulated benthic covers of coral and algae, and the biomasses of fish and urchins for a shallow (5-20m) coral reef habitat in each reef cell using a discretized weekly time step. We model nine functional groups: brooding corals, spawning corals, turf algae, grazed epilithic algal communities (EAC), herbivorous fish, small-to-intermediate ($< 60\text{cm}$) piscivorous fish, large ($\geq 60\text{cm}$) piscivorous fish, and sea urchins. Other benthic organisms such as soft corals, sponges, ascidians, and clams are assumed to make non-significant contributions to the dynamics we are attempting to capture and so are not modeled. Together, these organisms contribute to a proportional cover of benthic space. We have considered only those fish groups that are reef-associated. State variable 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' parameterizations, namely for the Indo-Pacific. A list of initial values, their description and sources are in Table 1; these are sourced predominantly from in-situ surveys within the main Hawaiian Islands (Rodgers et al. 2010). Empirical % coral cover values were partitioned as 75% broadcast spawning corals (producing and releasing gametes over a broad geographic area), and 25% brooding corals; historical percent cover was hind-cast to 20% greater than current values (Bruno & Selig 2007). A detailed exploration of equilibrium behavior and parameter sensitivities for both the local-scale, differential (continuous) system from which CORSET was derived, and the discrete-time equation array that constitutes the model used here, are each available in the Appendices.

Hurricane events were not forced during the validation aspect of this study, as they have not been a strong ecological driver in this region (Dollar & Tribble 1993; Dollar 1982), especially relative to Caribbean reefs (Dollar & Grigg 2004; Ostrander et al. 2000; Vroom & Timmers 2009; Gardner et al. 2005). Nutrification and sedimentation impacts were also not modeled as forcing events in checking for model accuracy.

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.

To test whether the model could accurately reproduce observed values for current community composition when provided real world events, 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 (Hoeke et al. 2011; De'ath et al. 2012; Osborne et al. 2011). We validated the model using real-world bleaching events from the last five decades using this mortality range, which affected the entire MHI in 1996, 2014, and 2015. 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 (Zeller et al. 2006). 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 ($\text{kg km}^{-2} \text{yr}^{-1}$) was calculated for each subregion (see Appendix). 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; this method was suggested by Zeller et al. (2006) as a simple method for historical catch reconstruction. In all sensitivity analyses, fishing pressure was assigned a value of zero throughout the model run.

For robust comparison, 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 (Rodgers et al. 2010), 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 parameterization 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 Melbourne-Thomas et al (2011) 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 (Oksanen et al. 2013) package in the R statistical program (R Development Core Team 2011). In all sensitivity analyses, fishing pressure was assigned a value of zero throughout the model run.

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 $\pm 10\%$ of their given value (Mumby et al. 2006; Melbourne-Thomas et al. 2011). 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 0.5km², 1km², 2km² 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 (0.5km², 1km², 2km² 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(Fung et al. 2011; Fung 2009). 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 (Melbourne-Thomas et al. 2011), 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.

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 S1-3.

138

139 **Figure S1A,B.** Principal components ordination of community composition under extreme values of benthic (A) and consumer (B) parameters. Three model runs to 100 years
140 were averaged for each parameter fixed at its maximum or minimum value. Radiating lines indicate state variable vectors (eigenvectors). In (A), 89% of the total variance is
141 captured by PC1 (75%) and PC2 (14%). Solid and dashed circles represent parameter's maxima and minima, respectively, for outlier values. Red circles = maximum coral growth
142 rate over macroalgae (relative to its growth rate over EAC), blue = minimum background mortality rate of brooding corals; green = growth rate of coral over EAC. In (B), 66% of

143 the total variance is captured by PC1 (46%) and PC2 (20%). Notable outliers are indicated by solid and dashed circles. Red circles = small piscivore death rate; green = the
144 proportion of small-to-intermediate piscivorous fish biomass that becomes large piscivorous fish biomass due to predation and subsequent growth; purple = minimum large
145 piscivore death rate; orange = maximum herbivore death rate.

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148 **Figure S2A,B.** Principal components ordination of extreme values of larval and forcing parameters. Solid and dashed lines represent parameter's maxima and minima,
149 respectively. In (A), 86% of the total variance is captured by PC1 (75%) and PC2 (14%). Red = extreme values of coral recruitment success, blue = extreme values of density
150 dependent mortality for fish and urchins. In (B), 69% of the total variance is captured by PC1 (51%) and PC2 (18%). Green circles = extreme values of sedimentation's scaling
151 factor upon coral mortality.

152

153 **Figure S3.** 100-Year trajectories for three benthic (top row) and three consumer (bottom row) parameters under “high-leverage” sensitivity analysis. Values are average annual
154 outputs from three model runs of 10 Monte Carlo simulations each. Colors highlight outlier trajectories; legend indicates which parameter was fixed at its extreme value for that

155 run. In general, benthic parameters are highly sensitive to coral growth and death rates (r_C , d_C); consumer parameters are heavily influenced by top-down predation factors
156 (g_{Pl} , g_{Ps}) and the growth rate of small piscivores into large (ϕ_{Ps}). For complete descriptions and ranges for all parameters, see Appendix.

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Induced Bleaching/recovery trajectories

We selected the top seven highest-leverage parameters, as indicated by eigenvalue scores from the sensitivity analysis, to evaluate their effect on recovery trajectories following a severe bleaching event at year 55. The outcomes from this examination are summarized in Table S3. Reef state recovered under high coral growth rates, fecundity and low coral mortality. It also recovered to its original state at both the minimum and maximum values of small piscivore graduation rate, and the density dependent mortality for fish in urchins, suggesting that these two parameters are less central to benthic regimes shifts. High coral mortality, low coral growth and fecundity rates and high piscivore biomass each induced a phase shift to an algal-dominated state. The MHI instantiation did not capture neither parameters relevant to the accessibility of algae to sea urchin nor herbivorous fish grazing as high-leverage, though they were found to be so in Meso-America. Instead, two new parameters regarding predation and growth of piscivores

Benthic Parameters		minimum	maximum
Coral death rate	d_C	●	▲
Coral growth rate over macroturf	alpha_C	▲	●
Coral growth rate	r_C	▲	●
Consumer Parameters			
Proportion of small-to-intermediate piscivorous fish biomass that becomes large piscivorous fish biomass due to predation and subsequent growth	phi_Ps*	●	●
The maximum predation rate of large piscivorous fish on herbivorous fish	g_Pl*	●	●
Death rate of herbivorous fish	d_H	●	●
Death rate of small-to-intermediate piscivores	d_Ps	▲	●
Death rate of large piscivores	d_Pl	▲	●
Larval Parameters			
Brooding coral fecundity	dlarv_C b	▲	●
Density dependent mortality rate for fish and urchins	drec_C	●	●

are deemed important in this region.

Table S3. Recovery responses for severe bleaching event under extreme values of high-leverage parameters. A triangle (▲) indicates the community underwent a coral-algal phase shift; a circle (●) indicates the community recovered to its previous state. Starred values were novel to this instantiation and were not identified as high-leverage in the Meso-American system.

Additional figures from the Model Validation

Figure S4A,B. Model trajectories for benthic and consumer variables, year 0 – 100, from 100 Monte Carlo simulations. With no forcings. CORSET demonstrates stable-state dynamics after ~30 years.

Figure S5. Subregional model trajectories for consumer (upper) and benthic (lower) parameters from 1965 to present from 100 Monte Carlo simulations. Dashed lines represent 95% confidence intervals for each year.

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6

7 **Figure S6.** Modeled 100-year trajectories from 100 Monte Carlo simulations following RCPs 4.5
 8 (dashed lines) and 8.5 (solid lines). Scenario Sweep: RCP 4.5 vs. RCP 8.5

9 For comparative purposes, we examined model trajectories across all state variables for
 10 two proposed emissions-mitigation scenarios, Representative Concentration Pathways 4.5
 11 (mitigation) and 8.5 (business as usual, (Riahi et al. 2011)). Both model runs were parameterized
 12 equally, with the exception that bleaching in RCP 4.5 occurs with a long-term, randomly
 13 generated frequency of twice per decade (Hoeke et al. 2011), which transitions to annually in
 14 year 2056; the same applies to RCP 8.5 with the transition occurring sooner, in 2056 (Van

Hooidonk et al. 2014). RCP 8.5 is unilaterally worse-off than the mitigations scenario; with high-trophic fisheries collapsing along with the coral community at large; the latter occurs to a lesser degree and later in RCP 4.5.

Figure S7. Modeled state variable responses for four marine protected area scenarios under RCP 4.5. Each panel represents a single response variable; individual boxes are color-coded by the percentage of reef cells closed to fishing activity.

Figure S8A,B. A) Fish biomass by island, in tons/hectare. B) Percent coral cover by island. Data from (Rodgers et al. 2015), representing mean values for years 2001-2008.

27 Additional Summary Tables & Figures for the Scenario Sweep

Scenario Name	RCP 4.5	RCP 8.5	RCP 8.5 + ntMPAs	RCP 8.5 + Nutrification	RCP 8.5 + ntMPAs + Nutrification
Fishing pressure	Between zero and 2x the mean reported value for the subregion	Between zero and 2x the mean reported value for the subregion	Between zero and 2x the mean reported value for the subregion; 5%, 10%, and 20% of reef cells completely closed to fishing take for model run	Between zero and 2x the mean reported value for the subregion	Between zero and 2x the mean reported value for the subregion; 5%, 10%, and 20% of reef cells completely closed to fishing take for model run
Coral Bleaching	Bleaching occurs in years 2009, 2014 and 2015 followed by a long-term frequency of twice per decade until year 2056, after which it occurs annually; mortality ranges from 0.05 – 0.15	Bleaching occurs in years 2009, 2014 and 2015 followed by a long-term frequency of twice per decade until year 2046, after which it occurs annually; mortality ranges from 0.05 – 0.15	Bleaching occurs in years 2009, 2014 and 2015 followed by a long-term frequency of twice per decade until year 2046, after which it occurs annually; mortality ranges from 0.05 – 0.15.	Bleaching occurs in years 2009, 2014 and 2015 followed by a long-term frequency of twice per decade until year 2046, after which it occurs annually; mortality ranges from 0.05 – 0.15.	Bleaching occurs in years 2009, 2014 and 2015 followed by a long-term frequency of twice per decade until year 2046, after which it occurs annually; mortality ranges from 0.05 – 0.15.
Nutrification	No modeled forcing	No modeled forcing	No modeled forcing	At each of 5%, 10%, and 20% proportion of reef cells are designated as “affected by nutrification”; the scaling factor for turf algae growth rate is 2 – 7; the scaling factor for coral larval production is 0.75 – 1.0	At each of 5%, 10%, and 20% MPAs, an equivalent proportion (yet not the same cells) are designated as “affected by nutrification”; the scaling factor for turf algae growth rate is 2 – 7; the scaling factor for coral larval production is 0.75 – 1.0

28 Table S4. Details of forcing conditions used in the scenario sweep.

Parameter	Low Nutrification (5%)	High Nutrification (20%)
Coral cover (%)	Nears collapse after 2075; generally higher than scenarios with more nutrification	Nears collapse after 2075; consistently lower than scenarios with less nutrification
Turf algae cover (%)	Increases over time; consistently higher than scenarios with more nutrification	Increases over time; consistently lower than scenarios with less nutrification
Macro algae cover (%)	Increases over time; consistently lower than scenarios with more nutrification	Increases over time, significantly & consistently higher than scenarios with less nutrification
Herbivorous Biomass (kg/km ²)	Generally stable over time	Generally stable over time
Piscivorous Biomass (kg/km ²)	Collapses after 2050; consistently lower than scenarios with more nutrification	Collapses after 2050; slightly higher than less-nutrient scenarios

TABLE S5. SUMMARY OF STATE VARIABLE RESPONSES TO VARIED NUTRIFICATION REGIMES WITHIN SCENARIO SWEEP.

Parameter	Low no-take MPA + Low Nutrification (5%)	High no-take MPA+ High Nutrification (20%)
Coral cover (%)	Nears collapse after 2075; consistently higher than more-impacted scenarios	Nears collapse after 2075; consistently lower than less-impacted scenarios
Turf algae cover (%)	Increases over time; indistinguishable from more-impacted scenarios	Increases over time; indistinguishable from lesser-impacted scenarios
Macro algae cover (%)	Increases mid-century, then returns to previous levels	Increases mid-century, then returns to previous levels
Herbivorous Biomass (kg/km ²)	Generally stable over time	Generally stable over time; consistently higher than scenarios with less protection
Piscivorous Biomass (kg/km ²)	Nearly collapses after 2050; consistently lower than more-protected scenarios	Nears collapse after 2050; slightly higher than scenarios with less protection

TABLE S6. SUMMARY OF STATE VARIABLE RESPONSES TO PAIRED NO-TAKE MPAS AND NUTRIFICATION REGIMES WITHIN THE SCENARIO SWEEP.

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