

A modeling tool to evaluate regional coral reef responses to changes in climate and ocean chemistry

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Abstract

We developed a spreadsheet-based model for the use of managers, conservationists, and biologists for projecting the effects of climate change on coral reefs at local-to-regional scales. The COMBO (Coral Mortality and Bleaching Output) model calculates the impacts to coral reefs from changes in average SST and CO₂ concentrations, and from high temperature mortality (bleaching) events. The model uses a probabilistic assessment of the frequency of high temperature events under a future climate to address scientific uncertainties about potential adverse effects. COMBO offers data libraries and default factors for three selected regions (Hawai'i, Great Barrier Reef, and Caribbean), but it is structured with user-selectable parameter values and data input options, making possible modifications to reflect local conditions or to incorporate local expertise. Preliminary results from sensitivity analyses and simulation examples for Hawai'i demonstrate the relative importance of high temperature events, increased average temperature, and increased CO₂ concentration on the future status of coral reefs; illustrate significant interactions among variables; and allow comparisons of past environmental history with future predictions.

Introduction

Coral reefs are one of the most threatened marine ecosystems and are under significant sources of stress in many locations (e.g., Knowlton 2001; Hoegh-Guldberg et al. 2007). These stresses include degradation of water quality from coastal dredging, construction, and runoff; over-harvesting of corals and associated organisms; and mechanical damage

from dynamite fishing, boating, and scuba diving (reviewed by Smith and Buddemeier 1992; Buddemeier et al. 2004). Wilkinson (2004) estimates that 20% of the world's coral reefs are dead, 24% are threatened with imminent collapse, and 26% are endangered on a longer-term basis.

These threats to coral reefs from direct human activities are magnified by the additional stress on reefs from climate change. Reef-building corals, the organisms that define and (along with other calcifiers) construct coral reefs, are invertebrates that secrete CaCO₃ exoskeletons and have an obligate symbiosis with intracellular algae (zooxanthellae). Rising global temperatures (e.g., Knowlton 2001; Hoegh-Guldberg 1999) are causing unusually high ocean temperatures. When combined with high light and calm water conditions, high temperatures are associated with an increased risk of coral bleaching, in which the vital symbiotic relationship breaks down. Although corals can recover from mild or moderate bleaching episodes, prolonged, intense, or repeated bleaching is likely to prove fatal to the host coral. Coral bleaching events resulting in high coral mortality appear to have increased in frequency and severity in the last 25 years as sea-surface temperatures (SST) have risen (Glynn 1993; Hoegh-Guldberg

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1999; Wilkinson 2004). Global climate change, driven largely by increasing CO₂ concentrations (Kleypas et al. 1999; Langdon et al. 2000), is also associated with increased acidification of the surface layer of the ocean, resulting from an increase in the amount of CO₂ that dissolves in the ocean. As the ocean acidifies, the concentration of carbonate ion in seawater is reduced, impeding the growth of corals by making it more difficult for them to form their calcium carbonate skeletons.

Faced with these threats, governments and agencies involved with climate change adaptation and mitigation need realistic estimates of potential coral loss within specific regions. Although coral reef managers are limited in their abilities to influence changes in global temperature and ocean chemistry, realistic forecasts will support developing management plans that will help reefs resist, recover from, and adapt to these stresses when possible, as well as supporting the adaptation of the human populations that interact with the reefs. A number of papers have been published addressing various aspects of coral responses and/or climate predictions (e.g., Ware et al. 1996; Hoegh-Guldberg 1999; Sheppard 2003; Wooldridge and Done 2004). However, these models either make very generalized global predictions (e.g., Hoegh-Guldberg 1999), are focused on a single stressor or region (e.g., Ware et al. 1996; Sheppard 2003), or are location-specific and/or data-intensive (e.g., Wooldridge and Done 2004), without a framework for adapting model results for convenient local use in other locations or specific situations. Also, most existing models have focused only on the impacts from high temperature stresses (i.e., coral bleaching) without considering threats to coral reefs from acidification and other changes in ocean chemistry (Kleypas et al. 1999).

Thus, new modeling tools are needed that

- incorporate long-term effects of changes in temperature and ocean chemistry on coral reefs together with the impact of short-term high temperature (bleaching) events;
- have flexibility to incorporate relevant regional or local data and expert judgment, and to allow scenario testing and habitat comparisons;
- can be used by biologists, reef managers, and policy-makers who lack resources and/or expertise for complex modeling or model development; and
- can be readily modified or linked to other models (e.g., socioeconomic impact).

Our objective in the work presented in this paper is to take a major first step toward meeting the anticipated need for a coral-climate ecosystem impact modeling and decision support tool. We have developed a flexible, user-friendly, analytical simulation model for predicting the potential effects on coral reefs of temperature increases and ocean chemistry changes caused by climate change. The COMBO model provides Coral Mortality and Bleaching Output. Three versions have been prepared, tailored to the conditions in the Hawai'ian archipelago, the Australian Great Barrier Reef, and the Caribbean region. The model honors the scientific com-

munity's accepted generalizations about coral behavior and response and provides default values and relationships for use in the target areas. However, it can be adapted to any region, as it also contains extensive options for input of local data, exercise of expert judgment, and modification of the underlying model structure by anyone familiar with spreadsheet calculations. Thus, the COMBO model both serves as a modeling or model development tool and provides a "ready-to-use" simulation model for areas and coral reef conditions represented by the default data inclusions, or for educational purposes. In its present form, it is oriented toward prediction of bleaching events of the type termed "physiological" by Fitt et al. (2001). However, it could easily be modified to address "shock" bleaching events having a more rapid onset but a lower total heat dose (Berkelmans 2002).

This paper and the supplemental material provide the scientific community with a detailed guide to the COMBO modeling tool. The COMBO model is a new method for assessing climate change impacts on coral reefs at regional scales. This method is freely available for adoption by the scientific and reef management community (information on how to download the model is provided in the *Methods* section). Fig. 1 illustrates the functional structure of the model. Below and in Web Appendix A, we describe, assess, and discuss the model operation, underlying assumptions, and calculation methods. As a major part of the assessment, we also present a sensitivity analysis for key model parameters and illustrate the model's capabilities with a simulation of change in coral reef cover in Hawai'i for 2000-2100, with comparisons to actual observations in the period 1990-present.

Materials and procedures

Data used—The COMBO model supplies future temperature and CO₂ scenarios for prediction of future sea surface temperature (SST) and CaCO₃ saturation state, and historic temperature records or reconstructions to characterize the environment to which the corals are assumed to be adapted. These provide initial values for the model runs as well as patterns of intra- and inter-annual variability to drive the probabilistic assessments. Details of the applications of these data and derived quantities are presented in the "Procedures" section (below).

Baseline monthly and annual temperature distributions—Monthly temperature patterns (the average monthly temperature deviation from the long-term annual mean) for oceanic conditions were derived by averaging offshore monthly temperatures for 1982-1999 from the Reynolds OIv2 blended temperature records (<http://iridl.ldeo.columbia.edu/SOURCES/.NOAA/.NCEP/.EMC/.CMB/.GLOBAL/>) for selected one-degree cells within each modeled latitude band (see following section and map pages, Web Appendix A).

Long-term variability of extreme temperature occurrences is represented by the three-month mean maximum temperature (the distribution of monthly deviations of the mean of a three-month running average of the monthly temperatures

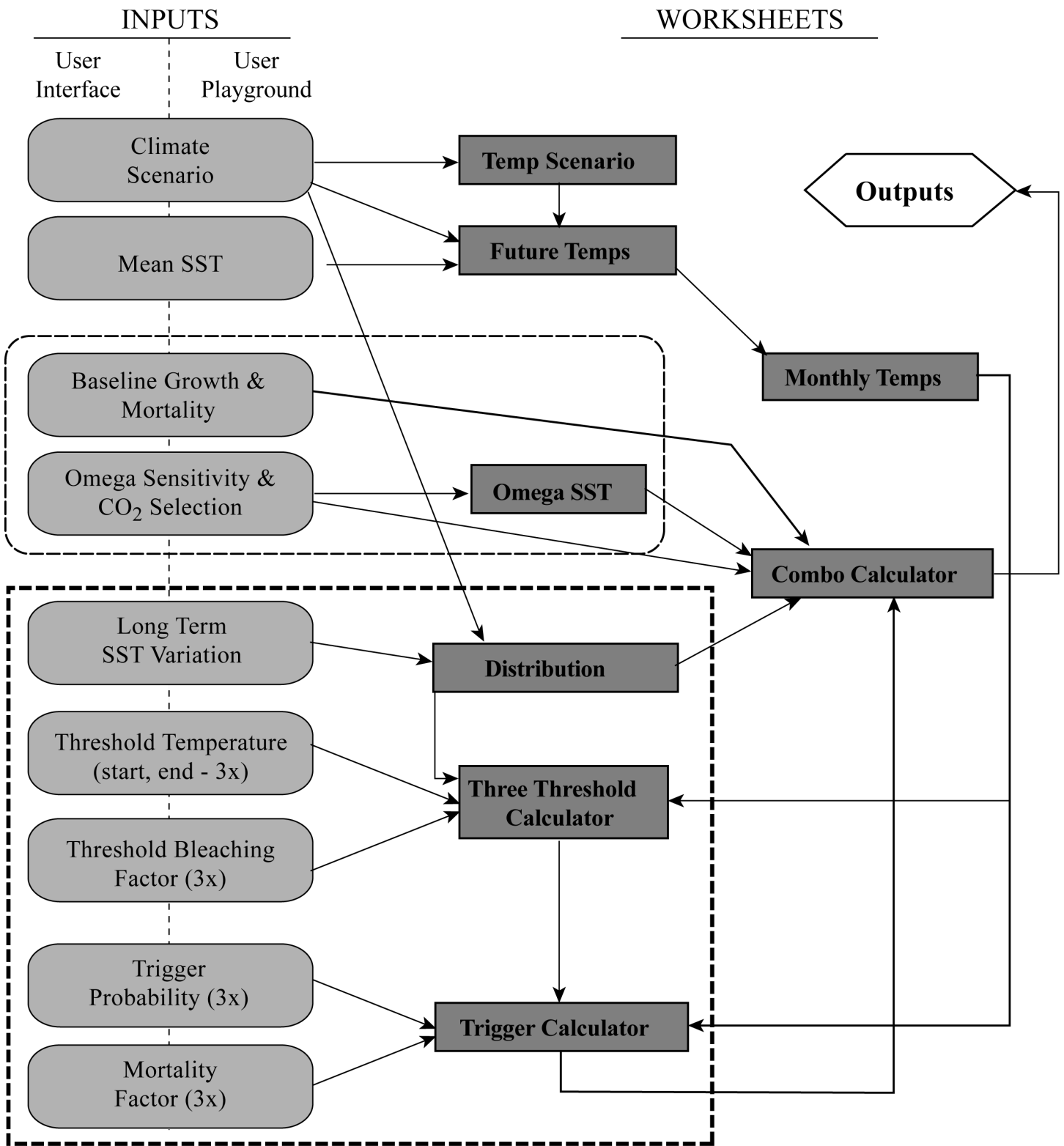


Fig. 1. Conceptual structure of the COMBO model. Items in the left-hand column represent input tables or selection menus that allow the user to set up the desired calculation. 3 × indicates that there are three different settings for that particular input (e.g., Threshold A, Threshold B, Threshold C.) The darker rectangles represent worksheets in the Excel COMBO workbook; these are the sources of the included datasets and the interactive calculations. Arrows indicate interactions within the model and show the direction of data flow. The dashed lines identify the two modules within the COMBO model: the long-term (average) change calculation module is at the top, and the episodic event module is at the bottom. See also Web Appendix A.

from the average of the annual three-month maximum values over the period 1900-1999). The annual three-month mean maximum temperatures were calculated for similarly selected one-degree cells (see map pages, Web Appendix A), using the HadISST global SST dataset (a product of the UK Hadley Centre (<http://badc.nerc.ac.uk/data/hadisst/>)). The HadISST data from 1982 onward are obtained from essentially the same raw data as the OIv2 dataset but use different algorithms in processing. Hindcast modeling has extended the HadISST dataset back to 1871 by linking to available historic SST measurements. Although synthetic in nature, these data provide a longer time series and a historic perspective unavailable in any directly measured dataset.

Patterns and distributions derived from locally measured surface temperature records are also included in the Hawai'i model. Monthly temperature patterns were derived from averaging monthly SST for 1993-2001 taken inside Kaneohe Bay, Oahu (Jokiell unpubl. data), and from averaging twice-weekly near-shore sea surface temperature for 1957-1991 taken at Koko Head, Oahu (National Marine Fishery Service unpubl. data; Jokiell and Brown 2004). The Koko Head record was also used to generate a distribution of high-temperature variations.

In addition, COMBO has an adjustable-amplitude sine wave option (cosine wave for Australia) that creates a regular pattern of monthly variation, and a normal distribution generator with adjustable standard deviation for interannual distribution experiments. User forms permit entry of other temperature patterns as well.

Future temperature and CO₂ scenarios—The user can select from five future climate scenarios to drive the model simulations or can enter temperature and/or CO₂ scenarios into tables provided. The library of future CO₂ and temperature scenarios was obtained from the MAGICC/SCENGEN (v. 4.1) global climate model (Wigley 2004). MAGICC is the “Model for the Assessment of Greenhouse-gas Induced Climate Change” and is a coupled gas-cycle/climate model. The IPCC used MAGICC as a primary model to project future increases in global mean temperature and sea level rise for the TAR, or Third Assessment Report (Houghton et al. 2001). SCENGEN, which is a “Global and Regional Climate SCENario GENerator,” combines results from MAGICC with regional climate change patterns obtained from 16 different General Circulation Model experiments, and then combines these with sulfate aerosol-induced patterns of climate change and with observed global and regional climate data sets. This creates spatially explicit patterns of temperature change for a common 5° latitude/longitude grid (Wigley 2004). Because COMBO uses 2000 as a base year for starting simulations, MAGICC/SCENGEN results were reported as °C above the temperature in the year 2000.

Results were obtained from MAGICC/SCENGEN for three emissions scenarios used in the TAR (predicted atmospheric CO₂ concentrations in 2100 are given in parentheses): B1 (540 ppm), A1B (703 ppm), and A1FI (958 ppm). Scenarios were

based on the default emission models: AIM for B1 and A1B, and M1 for A1FI. The atmospheric concentration of CO₂ in 2005 was 379 ppm. Each scenario was run in MAGICC/SCENGEN assuming a 3°C climate sensitivity to doubling of the preindustrial CO₂ concentration of 280 ppm. This was the “most likely sensitivity” reported in the IPCC Fourth Assessment Report (FAR) (IPCC 2007). In addition, the A1B (“business as usual”) scenario was run with additional climate sensitivities of 2°C and 4.5°C, which bracket the likely range of climate sensitivities discussed in the FAR.

Temperatures provided for the climate scenarios are lower atmosphere temperatures because SST are not available from the MAGICC/SCENGEN model. The temperatures used in COMBO are averages of the lower atmosphere temperatures for three “grid cells” that form a 5° latitude by 15° longitude rectangle and are considered representative of the region of interest. Lower atmosphere and SST predictions were compared using one of the General Circulation Models (HadCM2) that is incorporated into MAGICC/SCENGEN (B. Santer pers. comm.). The two temperature predictions differed by no more than 0.1° to 0.2° in the study areas. Thus, use of lower atmosphere predicted temperatures appears to be a reasonable approximation for SST.

For each regional version of COMBO, “grid cells” were selected that represent key locations for coral reefs in the area. It also was necessary to select cells that contained little or no land mass, because air temperatures are not good approximations for SST when a cell contains a large land mass. This criterion had no impact on cell selection for Hawai'i, and only a slight offset for the Great Barrier Reef. For the Caribbean, however, the cells used were actually western Atlantic cells at the same latitude as the Caribbean water bodies. A map showing the location of the selected grid cells is included with the COMBO model.

COMBO provides a library of CO₂ concentrations at five-year intervals obtained from MAGICC for the B1, A1B, and A1FI scenarios. The user can input individual CO₂ concentrations if desired, as well.

Baseline coral reef cover data—Coral reef cover data are not included in the model but are available separately and were used in the assessment reported in this paper. The data (percent of area covered by hard corals) were assembled for the three regions addressed by versions of the model (Hawai'i, Great Barrier Reef, Caribbean) with the objective of approximating conditions in the year 2000 and are contained in Web Appendix B. Data from 1998-2003 were cross-checked for consistency with other data and accuracy of coordinates, and classified as either deep (>5 m depth) or shallow reefs.

The Hawai'i data sets used in the assessment in this paper came primarily from the Hawai'i Coral Reef Initiative Monitoring Program (<http://www.hawaii.edu/ssri/hcri/>), augmented by data from ReefCheck (www.reefcheck.org; G. Hodgson pers. comm.). Methods for data collection are available at the Hawai'i Coral Reef Initiative Web site.

Temperature-controlled coral growth and mortality data—The underlying relationships of coral growth and mortality to temperature change in COMBO are based on meta-analyses of multiple controlled temperature experiments involving the Hawai’ian reef corals *Pocillopora damicornis*, *Montipora capitata*, *Porites lobata*, and *Fungia scutaria* (Jokiel and Coles 1977, Houck et al. 1977; Coles and Jokiel 1978). To standardize results across all species and experiments for comparison and combination, growth responses in each treatment were expressed as fractions of the maximum response observed in that experiment (Fig. 2). The growth data were fitted with a third-order polynomial ($R^2 \sim 0.55$; Fig. 2A). The curve was scaled to bring the curve maximum to a value of 1.0 (Fig. 2B). The growth maximum occurred at a temperature of $\sim 25.9^\circ$ (the approximate long-term mean sea surface temperature east of Oahu), with decreases at sublethal higher and lower temperatures. The scaled growth-temperature response curve developed for Hawai’i is

$$Gtemp = 1.13939 \times [(-0.0008517) \times (T^3) + (0.04285) \times (T^2) - (0.5046) \times (SST)] \quad (1)$$

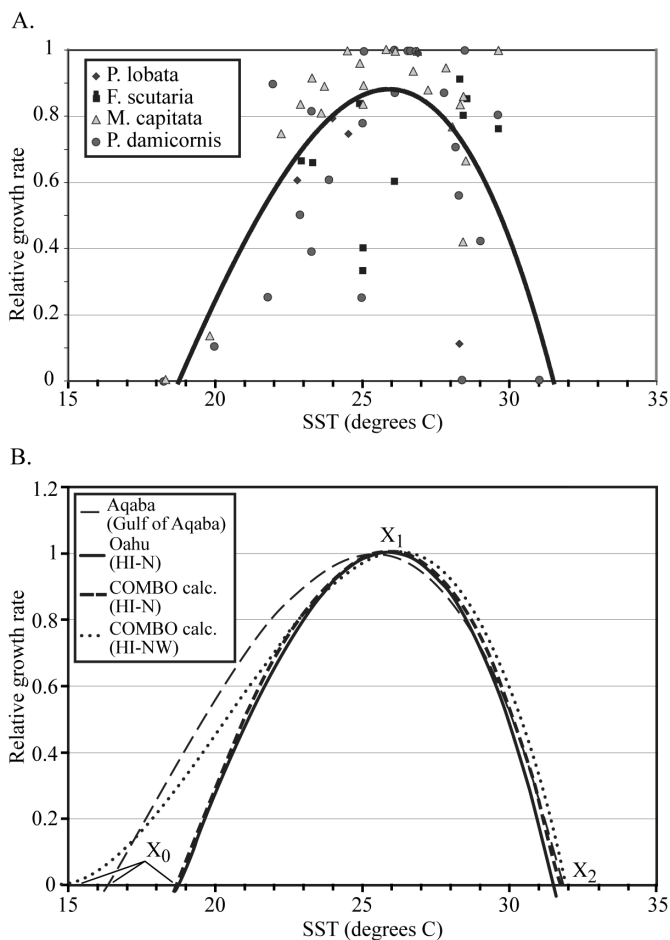


Fig. 2. A. Data points used in the growth-temperature meta-analysis and the fitted curve. B. The curve from A scaled to 1.0, a comparable experimental curve from the Gulf of Aqaba (Al Horani 2005), and two curves calculated as adjustments to reflect local temperature regimes. The points $\times 0$, $\times 1$, and $\times 2$ are the values used in curve adjustment (see text).

where *SST* is the monthly average sea surface temperature.

High-temperature mortality data from the Hawai’ian coral temperature experiments were modeled as a linear increase between 29.6°C and 31°C:

$$Mtemp = 0.60714 \times SST - 17.971 \quad (2)$$

In general, the corals in these experiments suffered high mortality below 19°C and above 31°C. At 31°C, mortality of three coral species (*P. damicornis*, *M. capitata*, *P. lobata*) ranged from 60% to 100%. Between 29.6°C and 31°C, coral mortality increased rapidly with increasing temperature.

Description of the model—The remaining sections of this paper describe the COMBO model, its operation, and present modeling results for the Hawai’i version of COMBO. Versions of COMBO have been developed for Hawai’i, the Great Barrier Reef in Australia, and the Caribbean; the structure of the model is identical for all three versions. Descriptions of the model and how to obtain a copy of it are available at <http://hercules.kgs.ku.edu/coralclimate/>. Web Appendix A contains an illustrated set of operating instructions, describing the mathematical/logical operations and assumptions involved in each major calculational step.

COMBO includes a probabilistic assessment of the effects of temperature increase and variance (intra-annual and inter-annual) on corals and coral reefs. Scales of applicability depend on the data inputs and the desired results; the default data provided are most relevant to time scales of decades and spatial scales of hundreds of kilometers (appropriate to the scales of climate processes and climate models).

Model design—The overall structure of the model is shown in Fig. 1. The long-term change module projects the impacts of changes in average SST and ocean chemistry on the growth and mortality of corals. The episodic event module calculates the cumulative probability of abrupt high-temperature stress events (“coral bleaching”), based on future temperature scenarios, intra- and inter-annual distributions of high temperatures derived from historical records, and user-selected values for factors controlling the heat dose and resulting mortality. To promote the goals of wide distribution and application by a range of users, Microsoft Excel was selected as the modeling platform. Running the basic model as provided requires no experience with computer programming.

Description—COMBO contains four types of functional components (Fig. 1):

(1) Input-output worksheets, where the user selects program and data options from those provided (User Interface) or substitutes preferred datasets (User Playground), and receives the coral cover calculation outputs in tabular and graphical form (User Interface and Numerical Output)

(2) Data storage and processing worksheets, containing selected future temperature and CO₂ scenarios, monthly temperature patterns, and distributions of interannual temperature variations based on historical records, as well as related calculational tools and derived products (CO₂ Library, Distribution,

Future Temps, Temp Scenarios, Growth Equations, Stats Summary, and Scenario Library worksheets)

(3) An extreme-event (e.g., bleaching) module that calculates the probability of exceeding a user-identified threshold and imposes the user-designated mortality when that occurs (Three Threshold Calculator and Trigger Calculator)

(4) A long-term change module that employs built-in or user-provided coral sensitivity and response options to calculate the effect of gradual temperature and saturation state changes on coral growth and mortality, and combines these with the output of the extreme event module to calculate the overall time trajectory of coral cover (Combo Calculator).

Change in coral reef cover is calculated as the difference between coral growth and mortality, accumulated in monthly time steps. Three factors affecting growth are modeled:

(1) Baseline growth (*Gb*): coral communities are dynamic entities, with cover determined by the balance between growth and recruitment on the one hand, and mortality on the other. The user selects an annual value for the fractional growth (including the effects of both organism growth and recruitment) that would be observed in the absence of mortality, and determines how that is apportioned among the months of the year (*Gmonth*).

(2) Temperature effects (*Geqn*) on growth are calculated from a growth-response equation (supplied by the model, but modifiable or replaceable by the user) that determines the effect of monthly temperatures relative to an empirically determined or assumed optimum value. For the initial 12 mo of a model run,

$$Gb = \sum (Gmonth \times Geqn). \quad (3)$$

Thereafter, the “baseline growth” term is modified according to the temperature and saturation state changes.

(3) Carbonate saturation state effects (*Gsat*) are calculated by determining the effect of the annual average aragonite saturation state on the monthly coral growth increments. Saturation state is estimated from the temperature and pCO₂ scenario values. *Gsat* is calculated for two user-specified sensitivity factors as well as for temperature only.

Similarly, the effects of three types of mortality are simulated:

(1) Baseline mortality (*Mb*), which is most simply characterized as “non-thermal” mortality (e.g., predation, storms, anthropogenic stresses, disease). The user selects an annual value and monthly pattern, as for *Gb*. For relatively stable communities, the steady-state assumption (*Gb* = *Mb*) is appropriate.

(2) Extreme event temperature effects (*Mevent*; bleaching-associated mortality): up to three mortality-inducing high temperature events can be modeled within each cover scenario calculation. Variables to be selected are discussed below.

(3) Systematic (gradual onset) temperature-induced mortality (*Mtemp*), which like *Gtemp* is calculated based on experimental observations. This may well represent mechanisms

similar to those involved in *Mevent* but is included for the convenience of being able to portray effects over different time scales. The user can choose to include or turn off the *Mtemp* calculation.

Based on the growth and mortality factors described above, the cover calculated for the *t*th monthly time step is

$$Cov_t = (Cov_{t-1} \times \{1 + [Geqn_t \times Gmonth_t \times Gsat_t - (Mb_t + Mtemp_t)]\}) \times (1 - Mevent_t) \quad (4)$$

where the terms are those described above.

Adjustment to other temperature regimes—The growth and mortality equations described above are appropriate for the O’ahu region of the Hawai’ian archipelago, but the temperature of maximum calcification, the upper lethal temperature, and other metabolic functions of corals have been shown to depend on the thermal characteristics of the coral’s environment (Clausen and Roth 1974; Coles et al. 1976). Locally relevant equations are needed for realistic models of coral growth and mortality in other locations.

The simple linear mortality equation can be adjusted by shifting the temperature of onset of thermal mortality. The default technique used in the model is

$$Mtemp = 0.60714 \times SST - [17.971 + (Tmmm - 29.6)/100], \quad (5)$$

where *Tmmm* is the mean maximum monthly temperature for the site of interest and 29.6°C is the monthly temperature value for the onset of mortality from the Hawai’i experimental data. The added term shifts the curve so that no significant mortality occurs until temperatures exceed the assumed local threshold by an amount equivalent to the difference between 29.6° and the local threshold in Hawai’i. The user can also enter a different adjustment factor on the User Playground or disable the *Mtemp* function so that all temperature-induced mortality will come from high-temperature events.

To adjust the more complex growth-temperature relationship, we developed a method to create a cubic growth temperature equation (similar to that derived for Hawai’i) based on local temperature characteristics. The COMBO growth curve and a calcification curve for a different coral species (*Galaxea fascicularis*) from the Gulf of Aqaba (Al Horani 2005; Fig. 2A) have similar relationships to key aspects of local temperature distributions. We developed a matrix equation in Excel (solved in the “Curve Equations” worksheet of the model) based on four conditions: growth (*y*) = zero at the low and high temperature *x*-axis crossing points (*x*₀ and *x*₂), growth = 1 at the temperature of maximum growth (*x*₁), and *dy/dx* = 0 at the temperature of maximum growth (*x*₁). Based on the O’ahu and Aqaba equations and local SST records, we determined: *x*₀ ≈ minimum mean monthly temperature – 5°; *x*₂ ≈ maximum mean monthly temperature + 5°, and *x*₁ ≈ maximum mean monthly temperature – 2 standard deviations. The model creates curves for temperature regimes selected from the built-in datasets; the user can also provide estimated or measured values for critical variables, or substitute a different equation.

Fig. 2B shows the two empirically derived curves (Gulf of Aqaba and O'ahu HI-N), plus two curves generated by COMBO. The COMBO HI-N curve was derived for comparison with the O'ahu empirical curve, using the O'ahu oceanic temperature distribution. The COMBO HI-NW curve is for the Northwestern Hawai'ian Islands (NWHI; e.g., Midway). The approximate locations of the various values of x_0 , x_1 , and x_2 are shown.

CO₂ effects: Calculation of changes in aragonite saturation state (Ω_a)—Omega values used in COMBO are derived from a lookup table (CO₂ Library worksheet) provided by Joan Kleypas, Scientist at the National Center for Atmospheric Research (NCAR). The table is a matrix of pCO₂ (in increments of 0.1 ppmv) \times SST (in increments of 0.5°), with the corresponding Omega values calculated using these assumptions for typical ocean water values: (1) Total alkalinity is constant at 2300 uequiv/kg; (2) silicate concentration is constant at 2.0 μ mol/kg; and (3) phosphate concentration is constant at 0.1 μ mol/kg. Dissociation constants are from Dickson and Millero (1987); saturation state was calculated according to Mucci (1983). We assumed that pCO₂ in the surface ocean equilibrates with pCO₂ of the atmosphere on approximately an annual time scale. Table 1 provides an example of COMBO calculations of Ω_a for a subset of values for partial pressure of CO₂ (pCO₂) and SST. Rising pCO₂ dominates the changes, causing a decrease in Ω_a but increasing temperatures partially compensate by causing a smaller reduction. The climate scenarios in COMBO (described above) yielded Ω_a values ranging from 2.2 to 3.0 over the various locations in the year 2100, compared with the present range of 3.6–4.0 (~3.67 near O'ahu).

Sensitivity of growth to changes in aragonite saturation state (Ω_a)—Saturation state sensitivity ($Sens_{\Omega_a}$) is defined as the decrease in growth per unit decrease in Ω_a , relative to an assumed maximum growth rate at $\Omega_a = 4.6$ (C. Langdon pers. comm.). Values of $Sens_{\Omega_a}$ in COMBO range from 0 to 0.4 (40%), selectable in increments of 0.05. The model calculates the response of corals to changes in Ω_a ($Gsat$) for two user-selected sensitivity values plus a temperature-only ("zero sensitivity") case. The use of different sensitivities reflects both scientific uncertainty and natural variability in the sensitivity of corals to decreased Ω_a (Langdon 2002).

Calculation of episodic high-temperature stress (bleaching events)—The episodic event (Bleaching Mortality) module calculates the impacts of episodic events on coral survival. This module models the effects of up to three high-temperature events (identified as a, b, and c), calculated as a series of nested probabilities. In addition to selecting climate change, monthly pattern, and interannual high temperature distribution scenarios, the user selects or inputs values for four other variables for each of the three events:

$TT(a,b,c)$ = Threshold Temperature values for heat-doses (degree-heating months) corresponding to possible bleaching events, which are expressed as the °C above the local mean max-

Table 1. Omega-aragonite (Ω_a) for various values of pCO₂ and SST

SST/CO ₂	280	370	540	700	800
25°C	4.31	3.67	2.88*	2.4*	2.18*
27°C	4.55	3.89	3.07	2.57*	2.34*
29°C	4.79	4.11	3.27	2.74*	2.5*
31°C	5.03	4.34	3.47	2.92*	2.67*

*Values <3.0 are considered marginal for reef growth (Guinotte et al. 2003)

imum 3 mo temperature. For example, a threshold temperature of 1°C above the local mean maximum temperature would correspond to 3 mo \times 1° = 3° mo ~ 12.9° weeks of stressful heat (10°–12° weeks is a common guideline for possible onset of bleaching mortality – (Liu et al. 2003; <http://www.osdpd.noaa.gov/PSB/EPS/SST/methodology.html>). In combination with the TT values, entries for $\Delta TT(a,b,c)$ permit defining amounts and rates (degrees/year) of temperature adaptation or de-adaptation associated with each event or interval.

$BF(a,b,c)$ = Bleaching Factor, a temperature-independent factor estimating the fraction of the high temperature events meeting the Threshold Temperature criterion that will actually cause the selected level of mortality (which typically requires sustained high light and low water motion as well as elevated temperature), based on local weather patterns.

$TP(a,b,c)$ = Trigger Probability. TP is the cumulative probability of occurrence of a mortality event (including the effects of both TT exceedance and BF) that the user has designated to identify as the temperature (and therefore time) point at which the mortality effect of the bleaching episode will be applied. For example, 50% estimates the time at which there is an even chance that the event will have already occurred; 95% or 5% might be used to identify times when one could be reasonably confident that an event of the specified magnitude had, or had not, occurred.

$MF(a,b,c)$ = Mortality Factor. MF is the fraction of the currently living coral cover that dies when the trigger probability for a specified bleaching event is reached. When that occurs the mortality fraction is subtracted from the value of the percent cover remaining at the end of the time step in which the trigger is 'pulled.'

Calculation of cumulative probability of threshold exceedance—COMBO first calculates the differences between the threshold temperatures and the sea surface temperature for each monthly time step,

$$Tdiff_{[a,b,c]} = TT_{[a,b,c]} - SST, \quad (6)$$

and then calculates the probability of that change in predicted average monthly value resulting in an observed temperature difference corresponding to one of the cumulative heat dose threshold values. This is done using the Excel PERCENTRANK function to compare the calculated difference with a distribution of variations around the mean of the maximum annual average 3-mo temperature for the location. The distribution can be selected from values provided

in the model that are drawn from historical record, provided by the user, or generated with a built-in adjustable normal distribution function.

Fig. 3 plots the distribution of differences between individual maximum annual 3-mo temperature values and the mean of those values. The illustration is from the HadISST1 dataset (see Section 2.6.4) for the period 1900-1999 in the one-degree cell centered at 21.5°N, 157.5°W. The two sets of bars compare the original distribution with the same distribution shifted to represent a 0.2° rise in average temperature.

When $Tdiff_{(a,b,c)}$ is larger than $Distrib_{Max}$ where $Distrib_{Max}$ is the most positive difference value in the distribution (Fig. 3), the probability of a threshold-exceedance event is assumed to be 0 – the maximum temperature experienced because of variability would still be less than the threshold (e.g., the case for threshold TTc and the original temperature distribution in Fig. 3). When $Distrib_{Min}$ (the most negative value in the distribution) $\geq Tdiff_{(a,b,c)}$ the probability of exceeding the threshold is considered to be 100% (Fig. 3). Once $Tdiff_{(a,b,c)}$ enters the range of values represented by the selected distribution, the probability of exceeding the threshold in a given month is calculated using the formula:

$$P_{T>TT(a,b,c)} = 1 - \text{PERCENTRANK}(\text{Distrib}, Tdiff_{(a,b,c)}) \quad (7)$$

In Fig. 3, for example, at 0.7°C above the original mean SST, the mean of the annual 3-mo warm period would coincide with TTa , and the probability of a bleaching event would be approximately 50% in each year.

The key parameter for COMBO's extreme event module is the cumulative probability of a bleaching event. First, the probability of a bleaching event in each year is calculated:

$$P_{bleach(a,b,c)} = P_{T>TT} \times BF_{(a,b,c)} \quad (8)$$

where $P_{bleach(a,b,c)}$ is defined as the probability of a mild, moderate, or severe mortality event and is the product of $P_{T>TT}$ (the cumulative probability of threshold temperature exceedance; Eq. 7) and $BF_{(a,b,c)}$ (the “bleaching factor,” which is the independent

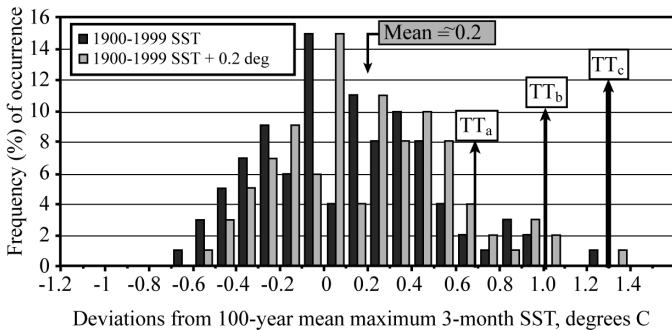


Fig. 3. Deviations from 100-year mean maximum 3-month SST (°C). The shift in bleaching probability with warming is illustrated; originally the fraction of the distribution above TTa is 7%, above TTb is 1%, and above TTc is 0. With a 0.2°C average temperature increase, the percentages shift to 9%, 3%, and 1% – corresponding to an increased probability that they will be exceeded in any given year.

probability that a given temperature event actually will result in bleaching).

To accumulate the effect of successive small probabilities over the years, we treat bleaching or nonbleaching occurrence in each year as an event independent of other years, and we calculate the cumulative probability of nonoccurrence of bleaching. Under these conditions, the cumulative probability of nonbleaching is simply the product of the successive individual annual probabilities, and the cumulative probability of bleaching having occurred by any given year is

$$\text{cumPbleach}_{(a,b,c)} = 1 - \text{cumPnonbleach}_{(a,b,c)} \quad (9)$$

where the cumulative probability of a “nonbleaching event” is given by the product of all of the probabilities of preceding “nonevents” times the calculated probability of the current nonoccurrence.

$$\text{cumPnonbleach}_{(a,b,c)} = \Pi(\text{Pnonbleach}_{y1}, \text{Pnonbleach}_{y2}, \text{Pnonbleach}_{y3}, \dots) \quad (10)$$

The value of $\text{cumPbleach}_{(a,b,c)}$ is tested continuously against TP , the specified trigger probability for the step in question. The first time $\text{cumPbleach}_{(a,b,c)} \geq TP_{(a,b,c)}$ the $n = 1$ event count causes the Survival Fraction factor in the Combo Calculator to be reduced by the fractional mortality (MF) selected for that threshold. Successive exceedances ($n > 1$) are ignored, which shifts the trigger function to the next higher threshold value.

Mortality application—Mortality associated with each event is modeled as a single event occurring at the time when the probability trigger is pulled. When $\text{TriggerPull}_{(a,b,c)} = 1$, a mortality event is imposed:

$$\text{Mevent}_i = MF \quad (11)$$

where MF is the user-defined threshold mortality factor $MF_{(a,b,c)}$ for that class of bleaching event.

The survival fraction for that month can then be defined simply as:

$$\text{Surv}_i = 1 - \text{Mevent}_i \quad (12)$$

where Surv_i is defined as the fraction of corals surviving the current bleaching event (if any).

A graduated step feature allows the user to distribute the mortality over as much as 10 y, following the step determination, and to include in the sequence of years negative mortality (i.e., recruitment). This permits consideration of complex interactions, such as bleaching followed by disease, or post-mortality recruitment events. This utility should only be used when the average temperature mortality function is disabled.

Integration of long-term change and episodic event modules—The Combo Calculator works on a monthly time-step with coral cover as a fraction of its baseline value calculated for each month. Rewriting Eq. 4 shows how the long-term change and episodic event modules are integrated

$$\text{Cov}_i = (\text{Cov}_{i-1} + \text{Gnet}_i) \times \text{Surv} \quad (13)$$

where the change in growth calculated in the long-term

change module can be expressed as

$$G_{net_i} = Cov_{i,1} \times [(Geq_{n_i} \times G_{month_i} \times G_{sat_i} - (Mb_i + Mtemp_i))] \quad (14)$$

The final output of the model displays three different time-series of changes in coral cover to compare the effects of different sensitivities to changes in saturation state, combined with the trajectory determined by responses to long-term and episodic changes in ocean temperature (Fig. 4). To arrive at this output, the user selects, accepts, or provides values for the variables described in Table 2. In this way, the modeling tool not only provides opportunities for site- or problem-specific design of the process, but also ensures that the user has considered the implications of all included variables.

Assessment

To illustrate the operation of the model, its straightforward integration of the effects of a complex suite of interacting parameters and the insights that it can provide, we have conducted a series of sensitivity analyses, and we use data from Hawai'i to address a simulation of future reef cover using recent bleaching history for comparison and calibration. For both analyses, we establish a basic climate change scenario, with modifications to reflect differences among local sites in the Hawai'i simulation. Table 3 summarizes the values used for the tests and simulations.

We stress that the heat doses selected are those inducing substantial mortality, rather than simply observable but non-lethal bleaching. For the sensitivity analysis, we have used a scenario producing a first mortality event in 2040 to provide room for shifting the response date in either direction by substituting different values for model variables.

Sensitivity analysis: temperature and CO₂ parameters—We conducted the parameter sensitivity assessment to explore potential responses of corals to changing temperature and CO₂ and to provide guidance for effective use of COMBO by identifying the parameters that have the greatest impact on results

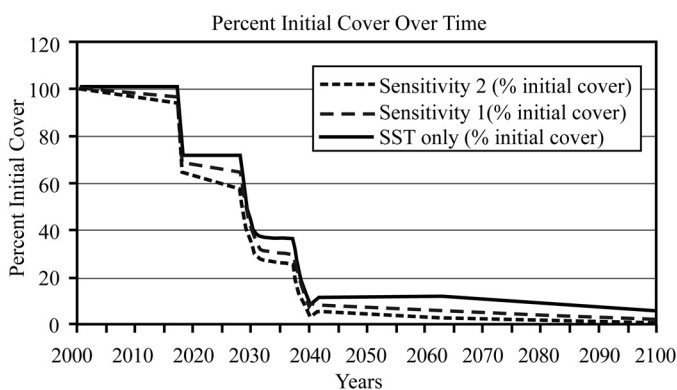


Fig. 4. Example of COMBO graphical output, illustrating features and variable effects based on Hawai'i data. For these model runs, baseline growth and mortality = 0.08 (8%), and the Graduated Step function was used to impose slightly different 5-y implementation patterns for each of the three mortality events.

and thus need the most attention in developing specific modeling scenarios. We evaluated the relative importance of saturation state and temperature in controlling responses within the long-term change module; the importance of various parameters in the episodic events module in controlling the predicted time or frequency of bleaching; and the relative importance of the outputs of the two modules in determining the overall changes in growth and cover.

Temperature and CO₂ in the long-term change module—Fig. 5 illustrates four different model outputs, showing the effects of SST only and of saturation state sensitivities (growth decline per unit decrease in Ω_a) of 20% (mid-range) and 40% (high). The first panel shows growth responses with no mortality from high temperature. This is simulated by setting the bleaching factor (BF) to zero and turning off the $Mtemp$ factor that simulates temperature-induced mortality in the absence of bleaching. The second panel adds the $Mtemp$ effect, the third shows the output for the Kaneohe Bay simulation with no $Mtemp$ and the three specified mortality events, and the fourth is the same as the third but with 8% substituted for 3% in the baseline growth and mortality.

In Hawai'i, mean monthly temperatures range from 23.5°C to ~27°C in the main Hawai'ian islands (MHI), and from <19°C to ~27.9°C in the Northwestern Hawai'ian islands (NWHI). Temperatures are more often below the optimal temperature for coral than above. Increasing average temperature therefore has an initial positive effect on growth, and even a warming of 2.6° by 2100 (the A1B scenario) only reduces cover by 15% if average temperature is the only factor affecting corals (Fig. 5A). When sensitivity to saturation state is considered, the year 2100 CO₂ values for the same scenario (710 ppmv) result in declines in cover of 41% for moderately sensitive corals (20% growth decline per unit decrease in Ω_a , compared with maximum growth at $\Omega_a = 4.6$), and a 60% decline in cover for high sensitivity corals (2 × the mid-range sensitivity value).

If the derived temperature mortality equation is applied, the corals die off rather precipitously over the course of 15 y starting in the late 2060s. We believe this abrupt change is at least partly an artifact of applying the results of multi-month constant temperature experiments to natural situations with varying monthly temperatures; we therefore ran the rest of the comparisons with the $Mtemp$ factor turned off.

The actual temperature effect observed may be more positive or more negative than these examples, and will depend on local temperature factors and the details of the growth-temperature response curve. However, if the effects of bleaching are excluded, in most areas the impact of increased CO₂ on coral cover will be much larger than the impact of long-term temperature increase until the upper lethal limit is approached.

The bleaching mortality events are discussed below, but a comparison of Figs. 5C and 5D show that the baseline values are important to the eventual responses even if the systems are

Table 2. List of parameters and options available to users of COMBO

Parameter	Built into Model	User Input	Notes
Temperature change	Climate scenarios based on MAGICC/SCENGEN simulations for B2, A1B, and A1FI SRES scenarios.	Yes*, monthly or 5-year values for interpolation; values or increments	
Start temp	Defaults to monthly pattern average	Yes*	
Pattern (monthly temperatures)	Values for selected cells from Olv2 dataset 1982-1999	Yes*, as monthly values or anomalies; also sine function	
Distribution (100 y monthly differences from mean SST)	Values for 1900-1999 for selected HadISST cells	Yes*; also as an adjustable normal distribution	Cells selected for reef position(s) within latitude band
CO ₂ change, 2000-2100	Concentration scenarios that correspond to B2, A1B, and A1FI SRES emission scenarios.	Yes*	Scenarios use a lookup table to determine saturation state
CO ₂ (saturation state) sensitivity – 2 values	0-0.4 by 0.05, % of max. growth decline per unit Ω_a	Yes, user selects value within range	Both selected sensitivities are displayed along with SST only effects
Baseline growth	0-0.1/y by 0.05	Yes, user selects value within range	
Baseline mortality	0-0.1/y by 0.05	Yes, user selects value within range	
Baseline growth and mortality patterns	Flat (equal fraction each month) or SST-scaled	Yes*	
Growth/cover as a function of SST	Equation based on HI data and adjusted for other local SSTs	Possible†	
Mortality as a function of SST	Equation based on HI data and adjusted for other local SSTs	Possible†	Can be disabled so bleaching is the sole source of mortality
Growth/cover equation translator	Cubic equation generator adapts the HI curve to local SST distributions	Yes*	
Threshold bleaching SST (3 steps)	User-entered values for the mean max 3-mo period	Yes*	Start and end values selectable to allow for “adaptation”
Trigger probabilities (3 steps)	Selectable 0-1 by 0.05	Yes, user selects value within range	Cumulative probability of occurrence at which mortality occurs
Bleaching factors (3 steps)	Selectable 0-1 by 0.05	Yes, user selects value within range	Fraction of specified temperature events resulting in the indicated bleaching
Bleaching mortality (3 steps)	Selectable 0-1 by 0.05	Yes, user selects value within range	Loss of cover when the bleaching event occurs

*User entry forms provided on User Playground or User Interface.

†Can be modified by straightforward replacement of values in a few cells in the calculational sheets.

Table 3. Summary of default parameters for Hawai'i tests and simulations

Parameter—all simulations	Value
Climate scenario	A1B with 3° sensitivity for doubled CO ₂
Baseline growth and mortality	3% per year
Interannual temperature distribution	Hawai'i-Average (HI-N and HI-S)
Trigger probabilities (<i>TP</i>)	0.5 for all steps
Mortality factors (<i>MF</i>)	0.3, 0.5, 0.7 for <i>MF_d</i> , <i>MF_y</i> , and <i>MF_c</i> respectively
Monthly pattern	HI-N (see text for discussion of secondary experiments)
Bleaching factor (<i>BF</i>)	<i>BF_σ</i> = 0.5, <i>BF_β</i> = 0.4, and <i>BF_c</i> = 0.3
—Sensitivity analysis	
Threshold temperatures (<i>TT</i>)	<i>TT_σ</i> = 28.2
Bleaching factor (<i>BF</i>)	<i>BF_σ</i> = 0.5
—Hawai'i simulation	
Threshold temperatures (<i>TT</i>)	<i>TT_σ</i> = 27.6, <i>TT_β</i> = 27.8, and <i>TT_c</i> = 28.0° for enclosed sites <i>TT_σ</i> = 27.8, <i>TT_β</i> = 28.0, and <i>TT_c</i> = 28.2° for protected sites <i>TT_σ</i> = 28.0, <i>TT_β</i> = 28.2, and <i>TT_c</i> = 28.4° for exposed sites

initially at steady-state. Both the growth-temperature and the saturation effect equations modify the growth rates proportionally, so the faster the initial baseline growth, the greater the absolute change in cover as it is cumulatively modified. To the extent that these are valid formulations of the actual process, these results imply that high-latitude or otherwise growth-inhibited reef communities may change less rapidly in response to long-term changes of climate than will the more luxuriantly growing corals.

Temperature factors controlling bleaching—As can be seen from Fig. 5C, when bleaching-induced mortality events are included, the impacts of these events on coral cover substantially outweigh the effects of both equilibrium temperature and saturation state. Understanding the controls on bleaching events, individually and interactively, is therefore critical.

A given probability of bleaching will depend on three temperature factors in addition to the threshold temperatures and the bleaching factors selected by the user. These factors are (1) the future temperature warming scenario, which is used to ramp up the monthly temperature pattern over time, (2) the interannual distribution of maximum temperatures which is compared with seasonal high temperatures, and (3) the selected threshold temperature. The probability of bleaching also will be modified by any adaptation that takes place.

Using the settings identified in Table 3, we established a base comparison scenario with a mortality event in 2040, and then tested the effects on the year of bleaching onset by substituting the other distributions of interannual temperature variation for the region, substituting the other climate change scenarios (B1-AIM-3°, A1B-2°, A1B-4.5°, and A1FI-3°), and substituting the other monthly patterns determined for Hawai'i and the northwest Hawai'ian Islands (NWHI). We also tested how the year of bleaching onset was affected by substituting different rates of adaptation to increasing temperature for the base scenario and for a more sensitive scenario with a mortality event in 2025. Fig. 6 summarizes how varying these factors

affects the years in which the first significant mortality occurs as a result of a high temperature event.

Changes in the monthly temperature pattern (intra-annual variation) exert a much stronger control (range of variation > 30 y) over the onset of bleaching than does the rate of change of average temperature (range of variation ~10 y). The results shown in Fig. 6 suggest that the long-term pattern of interannual temperature variation is even less important (range of variation < 10 y), at least for the regional examples considered here. These results translate directly to different sensitivities in locations where the temperature variations differ. For example, the monthly pattern in the Kaneohe Bay, a shallow enclosed body of water, has an average annual value slightly lower than the oceanic patterns, but the maximum monthly temperature is 0.5° higher. Adaptation rate, about which little is known, is potentially important because adaptation rates in excess of a degree per century can have a major effect on the onset of bleaching if the system is not too close to its first major mortality threshold. However, if such community-level adaptation occurs, it is likely to be punctuated, and in response to bleaching and partial mortality, rather than as the smooth function applied by the model (Glynn et al. 2001; Baker et al. 2004)

We examined the effect of varying the two user-set probabilities (Bleaching Factor [*BF*], and Trigger Probability [*TP*]) from 0.05 to 0.95. As described previously, *BF* is the fraction of high temperature events meeting the Threshold Temperature criterion that result in the selected level of mortality. Keeping other factors constant as described in Table 3, the first mortality events occurred in 2058, 2045, 2040, 2038, and 2037 for *BF* values of 0.05, 0.25, 0.5, 0.75, and 0.95, respectively. An increase in the fraction of “effective” heating events above 50% makes little difference, but shifting to substantially lower probabilities can significantly delay the mortality event. For the Trigger Probability, which is the cumulative probability of an event that the user has designated to identify as the point at which the mortality effect will be applied, the same

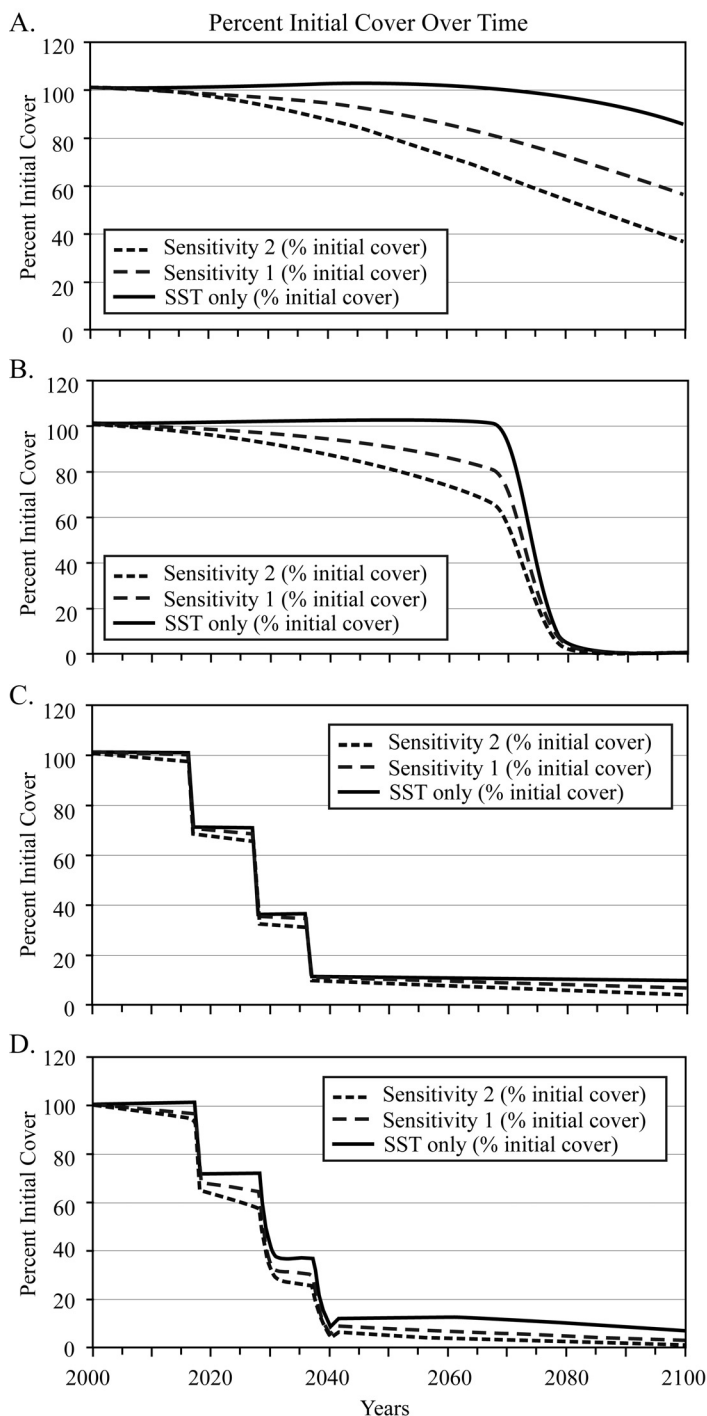


Fig. 5. Examples of COMBO graphical output, illustrating features and variable effects based on Hawai'i data. A. Effects on growth only of temperature and two sensitivities to Ω_a (0.2 and 0.4 – see text); no high temperature mortality is included. B. As in A, but with the long-term temperature mortality turned on. C. Three high-temperature mortality events simulated as step functions; baseline growth and mortality = 0.03 (3%). D. As in C, but with baseline growth and mortality = 0.08 (8%), and the Graduated Step function used to refine the time courses of the mortality events in slightly different ways for each of the three events.

sequence of probability values resulted in first mortality dates of 2028, 2036, 2040, 2045, and 2050. TP is more symmetrical than BF in the effects of its variation around 50%, with the lowest and highest values offering some sense of the time frames for identifying possibility and near-certainty.

Additional features of the COMBO model are signal generators that permit the user to substitute a variable-amplitude sine wave (cosine for the southern hemisphere) for the monthly pattern, and a normal distribution with an adjustable standard deviation for the interannual high temperature distribution. These functions are only approximate representations of the environmental variables, but they permit systematic experimentation. The monthly pattern amplitude (i.e., seasonal temperature range) has an approximately linear relationship to the date of event; the effects of changing the distribution range are nonlinear. Illustrations can be found in the relevant sections of Web Appendix A.

Model calibration and application to Hawai'i—To illustrate the exploratory and predictive capacity of the model, we calculated future coral cover on selected reefs of the Hawai'i islands of O'ahu and Molokai. We used the cover data for the year 2000 described above, and differentiated between the following reef environments: windward exposed, leeward exposed, windward protected, leeward protected, and enclosed. In the order listed, wave energy typically decreases, and water residence time increases, conditions consistent with increasing vulnerability to bleaching. For this example, we treated windward protected and leeward exposed as approximately equivalent.

In 1996, the enclosed or highly protected reefs in Hawai'i (primarily Kaneohe Bay) suffered the first major bleaching event recorded (Jokiel and Brown 2004). The bleaching was substantial and extensive, but it resulted in only very limited mortality. In 1997, incipient bleaching was observed, but it was interrupted by development of cloud cover. In 2004, bleaching was observed in a few of the most protected shallow areas. Substantial bleaching did not occur at the other reef environments that we considered.

To compare the observations with calculated and model-estimated heat doses, we used the HI-N dataset and the available Kaneohe Bay data to calculate and model the heat doses during each of those years. Three methods were used to calculate heat dose because there is no single established method:

- (1) We took the difference between the mean maximum monthly temperature and each observed monthly temperature from the appropriate record, and summed all positive values within each year;
- (2) We took the difference between the maximum observed 3-mo average temperature for the year and the mean maximum monthly temperature (the default method used in COMBO); and
- (3) We took the difference between the maximum observed 3-mo average temperature for the year and the mean maximum 3-mo temperature.

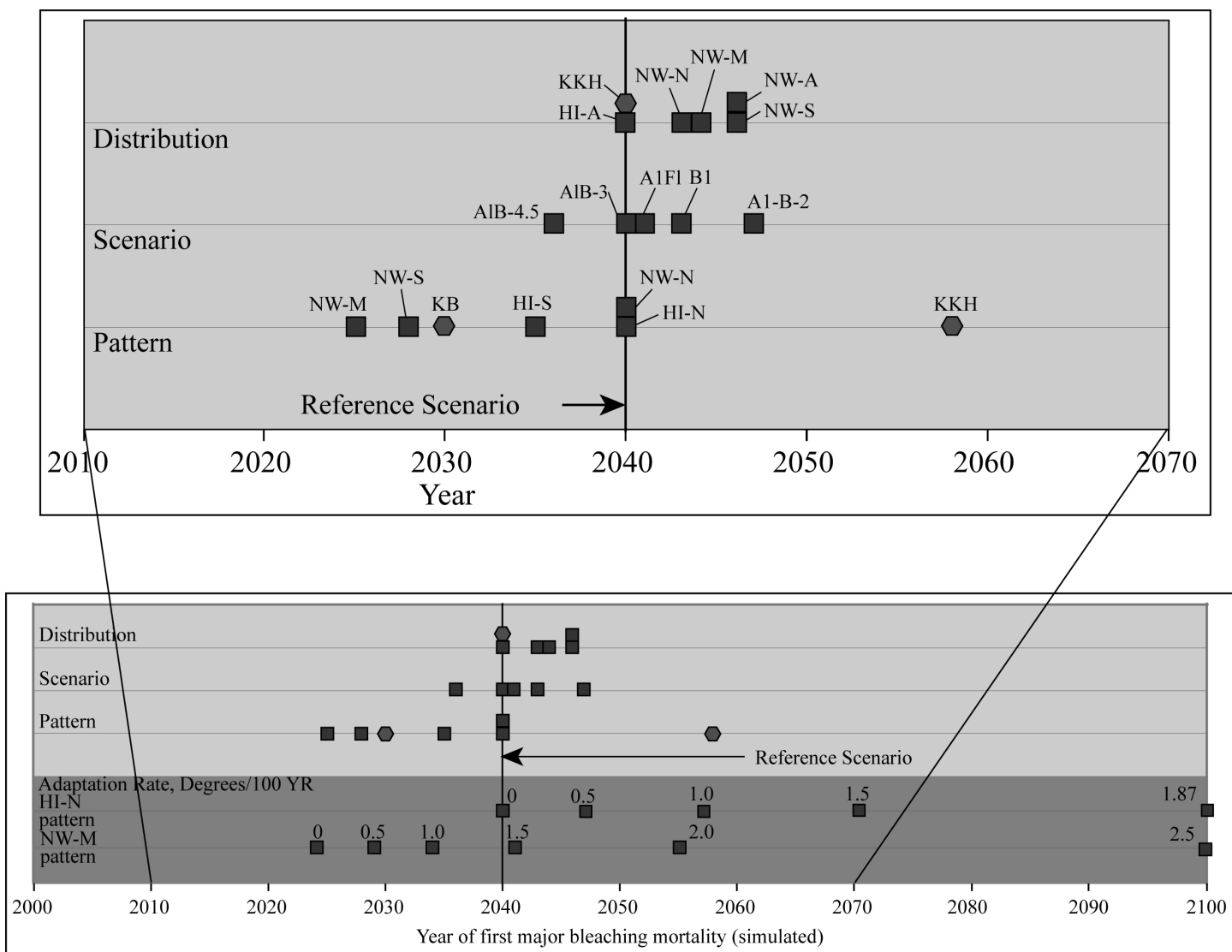


Fig. 6. Parameter sensitivity of a standard scenario mortality event date to substitution of other variable values from the same general region. The lower portion of the figure illustrates the effects of various adaptation rates ($^{\circ}\text{C}/100$ year) on two mortality scenarios with different initial dates. Hexagon symbols identify local point SST measurements; squares are blended regional data on a one degree grid.

In all three cases, we converted degree-months to degree-weeks (multiplied by 4.4). For Kaneohe Bay, we performed the calculations using both the oceanic and the KB baseline data to subtract from the KB observed temperatures. Table 4 summarizes the data and results; the three methods described above are identified as Calculated, Modeled 1, and Modeled 2, respectively.

Degree-weeks are a very approximate indicator of bleaching likelihood, but the rule-of thumb guidelines that are commonly used are that bleaching may be observed in the 4-8 degree-weeks range, with extensive bleaching possible at 8 and above. Significant mortality may occur starting at 10-12 degree-weeks. For the exposed reefs, the three calculation methods are in reasonable agreement and generally consistent with the lack of reported bleaching, although the “Modeled 2” results may slightly overpredict heat stress.

In the case of Kaneohe Bay, the calculated results tend to overpredict impacts, while the modeled results underpredict. Examination of the data suggests that the reason for both may be the duration of the warm periods in the Bay. In oceanic data records, it is rare to find periods longer than 3 mo that are consistently above the mean monthly maximum temperature. In Kaneohe Bay, positive deviations lasted 5 mo in 1996, four in 1997, and six in 2004. This means that a substantial part of the dose fell outside the modeled window; it also suggests that the gradual onset of a protracted period of moderately high temperatures may be less stressful than would be predicted on the basis of responses to a more rapid increase to a higher temperature of shorter duration (Berkelmans 2002).

The results that come closest to matching observations with dose value are the KB-baseline calculated in 1996, and

Table 4. Comparison of coral responses to heat dose for exposed and enclosed reefs

Parameter	Open ocean, HI-N (exposed reefs)	Kaneohe Bay, KB (enclosed reefs)	
SST data source	Reynolds Olv2 data for 1° cell at 21.5 N, 157.5 W (18 y)	Local temperature records, HIMB (11 of 13 years)	
Average (record)	25.28	25.13	
Mean max month	26.9	27.3	
Mean max 3 months	26.7	27.2	
Heat dose estimates (degree-weeks)			
Year	Oceanic observations versus oceanic baseline	Kaneohe Bay observations versus oceanic baseline	Kaneohe Bay observations versus Kaneohe Bay baseline
1996	No bleaching	Substantial bleaching	Minor mortality
	Calculated: 7.1	Calculated: 20.7	Calculated: 10.1
	Modeled 1: 7.1	Modeled 1: 5.0	Modeled 1: 2.8
	Modeled 2: 10.0	Modeled 2: 5.6	Modeled 2: 3.2
1997	No bleaching	Incipient bleaching	No mortality
	Calculated: 3.2	Calculated: 21.1	Calculated: 10.6
	Modeled 1: 2.9	Modeled 1: 5.7	Modeled 1: 3.5
	Modeled 2: 5.8	Modeled 2: 6.3	Modeled 2: 4.0
2004	No bleaching	Mild bleaching	No mortality
	Calculated: 6.3	Calculated: 35.6	Calculated: 23.8
	Modeled 1: 6.2	Modeled 1: 8.4	Modeled 1: 6.2
	Modeled 2: 9.1	Modeled 2: 9.0	Modeled 2: 6.6

either of the modeled results in 1997 and 2004 (~4°-weeks is a commonly used value for the onset of observable bleaching). The fact that the KB baseline data produce a more realistic estimate than the oceanic suggests that some local adaptation may be occurring. The examples of 1997 and 2004 (with almost no bleaching in spite of having heat doses as high as or higher than 1996) illustrate the importance of the Bleaching Factor, which sets the probability that a high-temperature event exceeding the heat-dose threshold will actually result in bleaching and mortality.

In order to model Kaneohe Bay directly, a considerably longer series of temperature data would be desirable. However, the results presented in Table 5 suggest that the ratio of the KB-baseline Kaneohe Bay heat dose to the oceanic-baseline dose is reasonably consistent. Combining all 14 data pairs (both modeled and calculated) yields a KB/Oceanic dose ratio of 1.67 ± 0.24 . To arrive at the Threshold Temperature values in Table 3, we selected a value of ~15 degree-weeks as the first mortality-inducing heat dose for exposed reefs and used the above ratio to estimate oceanic doses of 9°- and 12°-weeks for an equivalent dose of 15°-weeks on enclosed and protected reefs, respectively.

The results of the modeling are shown in Table 5 and as 20-y time slices in Fig. 7, with the reef site symbols color-coded to reflect original cover and successive reductions in cover over time. The exposed reefs and protected reefs show some loss after 2020 and near-complete collapse between 2040 and 2060. The enclosed reefs are damaged by 2020 and devastated by 2040. Similar results can be obtained without using the empirical calibration; in Table 5, the second “enclosed” entry

used the same TT values as exposed, but applied the Kaneohe Bay monthly pattern. The time-slice depiction masks the fact that the protected reef transitions are 5-10 y earlier than those of the exposed reefs, but it has the advantage of illustrating both the duration and locations of persistence of viable reef communities. This temporal-spatial information is important for identifying and managing reserves and for evaluating recruitment potential.

Discussion

Definitive assessment of tools designed to support predictive modeling or decision-making is challenging, because there is typically no alternative standard approach or “right answer” for comparison. Some of the criteria that can be used to determine whether the COMBO model does, or can, fulfill the objectives stated in the Introduction are as follows:

- (1) Does the tool provide a unique or greatly improved capability that is not otherwise available?
- (2) Does it address and integrate the essential concepts and parameters in a realistic and practical fashion?
- (3) Can it be used to produce useful comparisons, tests, or scenario evaluations?
- (4) Can it produce simulations compatible with observed phenomena, given reasonable and available input data?

The COMBO model clearly satisfies the first criterion. It was created because there is no known tool that satisfies the objectives stated in the Introduction. We assert that, subject to the limitations and potential additions addressed below, it also meets the second criterion based on the descriptions and citations presented in the *Materials and methods* section. However,

Table 5. Mortality event dates for the Hawai'i simulations

Reef type	Dates of predicted mortality events		
Exposed	2034	2042	2050
Protected	2026	2035	2044
Enclosed (1)*	2017	2028	2037
Enclosed (2)†	2020	2031	2040

*Enclosed (1) is calculated as indicated in Table 3.

†Enclosed (2) uses the exposed TT values and the monthly pattern from Kaneohe Bay.

both of the first two questions can only be fully answered by the experience and reactions of the eventual user community. We have also provided a means (the distribution Web site) by which community feedback, developments, and updates can be shared over time.

Criteria 3 and 4 are addressed in the Assessment section of this paper. The question of useful comparisons, tests, or scenario evaluations can be simply summarized by reference to Figs. 5 and 6, and Tables 4 and 5. The data for these tables and figures (or in the case of Fig. 5, the actual graphical as well as numerical output) were generated and assembled in a modest fraction of an hour. Testing one's own data rather than the library values would require some data formatting and entry, but the effort would still be trivial compared with making such

comparisons without the COMBO tool. In addition to the first-order comparisons illustrated in the figures, the effects of any desired combinations of the parameters addressed in Fig. 6 and Table 4 can be systematically examined and cross-compared with minimal effort. The straightforward graphical and tabular output of growth/cover over time is readily understood by both technical and lay audiences. Using a standardized calculational framework means that a simple table of values used (e.g., Table 3 above), reference to the published description, and notations of any modifications should suffice to specify the calculation methods for comparison or publication.

The COMBO model does not change our fundamental understanding of coral and reef sensitivity to climate change: high temperatures, high rates of temperature increase, and high CO₂ concentrations are more dangerous than lower values, and combinations of high values are more dangerous than elevation of a single variable. COMBO does, however, provide both a means of assessing the interactions of hazards in ways that can be more specific to local conditions and populations, and it provides a basis for analysis of relative risk associated with specific factors or with specific categories of ignorance or uncertainty.

A number of specific insights gained can be identified. One example is the importance of both seasonal and interannual SST variability in determining the probability of bleaching

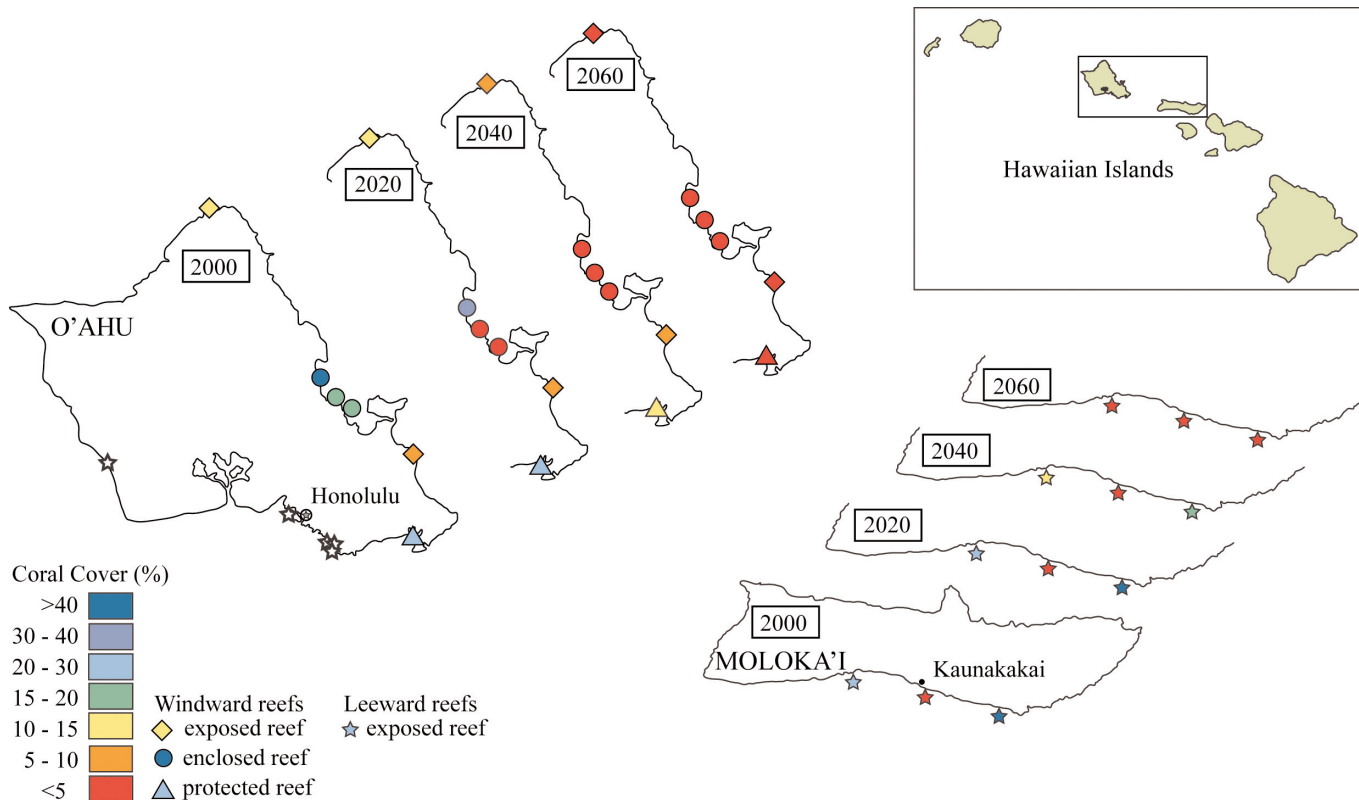


Fig. 7. Four time slices representing projected cover on selected reef environments on the Hawai'i islands of O'ahu and Molokai. Model scenarios used are given in Table 3. The environmental characteristics of specific reef habitats have a strong influence on the rate of degradation with increasing stress.

under any of the scenarios. These important variables are aspects of future climate that are not well-constrained or readily predicted. A related point is the importance of locally relevant information, both quantitative and qualitative, and the wide range of conditions that can occur over relatively short distances. The KKH and KB datasets (local point measurements) differ substantially from the blended regional data and cause substantial shifts in the results when used. Information of this sort can be used to support the selection of sites for focused conservation efforts and to identify the targeted research and monitoring needed to refine such selections.

The implication of some degree of local adaptation (although not enough to escape bleaching) by Kaneohe Bay corals supports other observations (e.g., Berkelmans 2002), and adds an important dimension to management and conservation considerations. Overall, the results show the importance of detailed, locally relevant modeling. The global average estimate that temperatures will exceed the bleaching threshold annually by 2030 (Hoegh-Guldberg 1999) seems both oversimplified and overly pessimistic when a more nuanced evaluation is made using local observations and appropriate data. COMBO permits a significant step toward facilitating such refinements.

Comments and recommendations

The adaptability of COMBO makes it primarily a modeling tool, with output applications and utility that will be determined more by the user than by the characteristics of the model itself. The model contains extensive possibilities for user choice and “what if” scenarios. The model is constructed so that the more experienced user can easily substitute other equations, parameters, or data sets for those supplied. Table 2 summarizes the user options available.

Adapting COMBO to other locations—In addition to the Hawai'i model described here, versions of COMBO have been developed for the Great Barrier Reef and Caribbean regions. These models are available for download from the source described previously and include library values of regionally appropriate temperature scenarios, distributions, and seasonal patterns. In addition, the model can be readily adapted for any other location, including locations within the regions for which the general models exist but where there may be local data or conditions that require modifications to the regional predicted or historic temperature or CO₂ scenarios. An example of this is included in the Hawai'i model, where local SST measurements provide results that differ from oceanic values for some nearshore locations (e.g., Kaneohe Bay). All temperature and CO₂ pattern data can be readily replaced, either on the User Playground sheet or directly in the calculation worksheets. Growth and mortality equations are automatically adjusted for applications to different long-term temperature regimes, but they can also be modified or replaced individually within the worksheets.

Model capabilities and limitations—There are recognized limitations to the use of COMBO. Some of these may be the subject of further modifications, but all of them can be at least partially addressed within the capabilities of the present version.

The present version lacks specific components dealing with climate-induced changes in reproduction and recruitment. These functions are known to be sensitive for some calcifying organisms (Kuffner et al. 2008) and are important to growth functions used to approximate cover. This lack can be compensated for by adjusting the growth and mortality functions used, but the most attractive way to do this would be to build in progressive changes in either the governing equations or the baseline rates, or both. At present, this would require either hand adjustments to the appropriate data columns or designing some new functionalities into the worksheet.

The assumptions of constant baseline growth and constant baseline loss occurring only through mortality and growth decline are optimistic and will yield conservative results, independent of the effects related to reproduction and recruitment. In addition to compensating for this by the modifications mentioned above, the CO₂ concentration scenario or one of the sensitivities could be redefined and modified to provide for an additional cover decrement with the desired temperature or saturation state dependence.

A secondary limitation in the model is the implementation of bleaching mortality only for three discrete steps, and on the basis of cumulative probability. The curve-smoothing option permits developing a more realistic cover trajectory for an individual event, and even building in some recovery effects. In addition, the number of steps could be expanded indefinitely (albeit in a somewhat cumbersome fashion) by simply replicating the existing structures and functions in the spreadsheets.

Other desired applications can generally be achieved by use of the User Playground options, by overwriting the built-in data and relationships, or by incremental modeling (e.g., running the model with one set of parameters up to a specific time or condition, then resetting the starting conditions and parameter choices for a subsequent segment).

Finally, we point out that the mathematical functions built into the model are independent of the labels attached (as noted in the possible redefinition of a CO₂ response to represent other sensitivities). In particular, the episodic mortality module could be used to represent episodic storm or runoff damage in exactly the same way it represents temperature excursions.

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