Journal name: Ecological Applications

Manuscript type: Article

Manuscript title: Multi-Factor Coral Disease Risk Forecasting for Early Warning and

Management

Author Names: *Jamie M Caldwell[1,2], Gang Liu[3], Erick Geiger[3,4], Scott F Heron[5], C Mark

Eakin[6], Jacqueline De La Cour[3,4], Austin Greene[1,7], Laurie Raymundo[8], Jen Dryden[9], Audrey

Schlaff [9], Jessica S Stella[9], Tye L Kindinger[10], Courtney S Couch[11,10], Douglas Fenner[12],

Whitney Hoot[13], Derek Manzello[3], and Megan J Donahue[1].

1. Hawai□i Institute of Marine Biology, Kāne□ohe, HI, USA

2. High Meadows Environmental Institute, Princeton University, Princeton, NJ, USA

3. NOAA/NESDIS/STAR Coral Reef Watch, 5830 University Research Court, College

Park, MD, USA

4. Global Science & Technology, Inc., 7501 Greenway Center Drive, Suite 1100, Greenbelt,

Maryland, USA

5. Physical Sciences and Marine Geophysics Laboratory, College of Science and

Engineering, James Cook University, Townsville, Queensland, Australia

6. Corals and Climate

7. Woods Hole Oceanographic Institution, Woods Hole, USA

8. University of Guam Marine Laboratory, Mangilao, Guam

9. Great Barrier Reef Marine Park Authority, Townsville, Queensland, Australia

10. Pacific Islands Fisheries Science Center, National Marine Fisheries Service, National

Oceanic and Atmospheric Administration, Honolulu, HI, USA

11. Cooperative Institute for Marine and Atmospheric Research, University of Hawai☐i at

Mānoa, Honolulu, HI, USA

12. Lynker Technologies, LLC, Contractor, NOAA Fisheries Service, Pacific Islands

Regional Office, Honolulu, HI USA

13. Guam Coral Reef Initiative, Government of Guam, Hagatña, Guam

*Contact and corresponding author

Keywords

Coral reefs, disease, machine learning, ecological forecasting, quantile regression forests

Open research statement: Data are already published and publicly available, with those items

properly cited in this submission. All code used to create the disease models are available at:

https://github.com/jms5151/Fore-C_v2/tree/main/Fore-C_v2/codes. All code and data used to

create the weekly prediction updates are available at: https://github.com/jms5151/Fore-

C_v2/tree/main/Fore-C_v2/operational. All code and data used to create the data explorer are

available at https://github.com/jms5151/uh-noaa-shiny-app. NOAA NCRMP fish survey data:

https://www.fisheries.noaa.gov/inport/item/28844;

https://www.fisheries.noaa.gov/inport/item/34515. NOAA NCRMP benthic survey data:

https://doi.org/10.7289/v53n21q5, https://doi.org/10.7289/v579431k,

https://doi.org/10.7289/v5c24trh, https://doi.org/10.7289/v5zw1j8b. Upon acceptance, all

underlying data and code pertinent to the results presented in the publication will provided via

Zenodo.

Abstract

Ecological forecasts are becoming increasingly valuable tools for conservation and management.

However, there are few examples of near-operational forecasting systems that account for the

wide range of ecological complexities. We developed a new experimental coral disease

ecological forecasting system that explores a suite of ecological relationships and their

uncertainty and investigates how forecasts operationally change with shorter lead times. The

Multi-Factor Coral Disease Risk product uses a combination of ecological and marine

environmental conditions to predict risk of white syndromes and growth anomalies across reefs

in the central and western Pacific and east coast of Australia and is available through the U.S.

National Oceanic and Atmospheric Administration Coral Reef Watch program. This product

produces weekly forecasts for a moving window of six months at ~5 km resolution based on

quantile regression forests. The forecasts show superior skill at predicting disease risk on

withheld survey data from 2012-2020 compared with predecessor models, with the biggest

improvements shown for predicting disease risk at mid- to high-disease levels. Most of the

prediction uncertainty arises from model uncertainty and therefore prediction accuracy and

precision do not improve substantially with shorter lead times. This result arises because many

predictor variables cannot be accurately forecasted, which is a common challenge across

ecosystems. Weekly forecasts and scenarios can be explored through an online decision support

tool and data explorer, co-developed with end-user groups to improve use and understanding of

ecological forecasts. The models provide near real-time disease risk assessments and allow users

to refine predictions and assess intervention scenarios. This work advances the field of ecological

forecasting with real world complexities, and in doing so, better supports near term decision

making for coral reef ecosystem managers and stakeholders. Secondarily, we identify clear needs

and provide recommendations to further enhance our ability to forecast coral disease risk.

Introduction

Forecasting coral disease outbreaks is critical for the timely management of reef

ecosystems, but developing such early warning systems is challenging when disease dynamics

are not well understood, and data are sparse and irregularly updated. Coral reefs and their

associated threats are a prime example of a complex system that presents challenges for

ecological forecasting. Coral reefs are dynamic, heterogeneous environments, characterized by

their diversity of species and species interactions, and physical and chemical factors that can

affect their health. Diseases are a major threat to coral reefs, causing up to 95% mortality in

dominant coral species during outbreak events such as the white band disease epidemic in the

1980s and 1990s and the Stony Coral Tissue Loss Disease outbreak in the 2010s and 2020s in

Florida and the Caribbean (Rosales et al., 2020; Walton et al., 2018). Thus, innovative

approaches to support effective management strategies for coral disease transmission,

prevention, and mitigation are urgently needed. Modern forecasting can now combine

mechanistic understanding, statistical and machine learning models, and the quantification of

uncertainty to make more accurate predictions. However, developing accurate and reliable

forecasts requires overcoming several key challenges, including the sparse availability of high-

quality data and limited understanding of the underlying complexity of biological and

environmental drivers of coral disease outcomes.

Developing early warning systems for coral diseases is a relatively recent endeavor that

aims to help managers and decision-makers take preventative actions and mitigative measures.

Given the widespread consensus linking coral disease to thermal condition, early disease

forecasts focused on using temperature to predict suitable conditions for disease. The U.S.

National Oceanic and Atmospheric Administration Coral Reef Watch (NOAA CRW) program

developed the first coral disease forecast in 2010 for white syndromes on the Great Barrier Reef

(GBR) in Australia (hereafter V1), which uses a decision tree framework based on a series of

anomalous thermal metrics (Heron et al., 2010). This system leveraged NOAA CRW's

established satellite sea surface temperature (SST) monitoring data (~50 km resolution, twice-

weekly) refining previous information about the relationship between thermal condition and

disease (Bruno et al., 2007; Selig et al., 2006). Subsequently, NOAA CRW adapted the thermal

condition metrics from the GBR to produce a complementary, experimental predictive tool for

coral disease in the Hawaiian archipelago (incorporated into V1). V1 was further developed to

incorporate finer resolution (~5 km, daily) SST data (hereafter V2). A retrospective analysis of

V2 demonstrated that machine learning algorithms that used the product metrics (i.e., summer

Hot Snaps) combined with additional biotic data could robustly reproduce disease prevalence

patterns for two coral diseases across three host species (Caldwell, Heron, et al., 2016). The

ability to nowcast and forecast some of these reef stressors has led to new and innovative

conservation practices and provided clarity to managers seeking to set priorities. While we know

of no examples yet where management officials have taken action in response to disease

forecasts, we have seen responses to NOAA CRW bleaching forecasts (e.g.., Raymundo L,

Andersen M, Moreland-Ocho...) and we expect complementary actions (e.g., Beeden et al. 2012;

Neely et al. 2021) will be taken in response to disease forecasts as managers become more

comfortable with their accuracy.

114  Moving beyond thermal conditions, the next generation of coral disease early warning

115 systems needs to better incorporate an expanded suite of conditions known or hypothesized to

116 affect disease dynamics. Previous research has statistically linked a range of conditions with

117 impaired coral health, including colony size and density, thermal condition, water quality, human

118 population density and land use, and fish densities and predation (Greene et al. 2020; Caldwell et

119 al. 2020; Carlson et al. 2019; Bruno et al. 2003; Haapkylä et al. 2011; Aeby et al. 2011; Aeby et

120 al. 2011; Pollock et al. 2014; Renzi et al. 2022; Redding et al. 2013). However, the mechanistic

121 underpinnings of these multiple contributing factors are often poorly understood due to their

122 complex and non-linear behavior, which can vary by host species and disease type (Clemens &

123 Brandt, 2015; Shore & Caldwell, 2019; Vega Thurber et al., 2014). An additional challenge for

124 any early warning system is whether the predictor variables themselves can be forecasted (Clark

125 et al., 2001; Oliver & Roy, 2015), and this is especially true for the diverse drivers of coral

126 disease. These challenges must be addressed to incorporate a wider range of putative disease

127 drivers into forecasting models.

128  Over the last decade, ecological forecasting and monitoring tools have advanced

129 considerably, making it possible to integrate multiple data streams and more robustly consider

130 various scenarios and sources of uncertainty (Clark et al., 2001; Dietze et al., 2018). Machine

131 learning algorithms are particularly useful in this context, as they can identify complex non-

132 linear relationships between variables and make predictions in data-poor environments (Jordan &

133 Mitchell, 2015). The resulting models can identify relationships that should be tested further,

134 allowing incremental improvements in forecasting efforts (Dietze et al., 2018). Exploring likely

135 scenarios within a forecasting framework can help create more robust approaches for managing

136 ecosystems. Plausible scenarios with alternate conditions are developed using a combination of

scientific information and models, stakeholder input, and expert opinion. Scenarios can then be

used to explore the potential impacts of different management strategies, account for additional

spatial variation in predictor variables, or refine predictions to a specific set of conditions. By

incorporating scenarios into ecological forecasts and management plans, managers and decision-

makers can better understand the potential outcomes of different decisions and identify strategies

that are more likely to be effective under a range of possible futures (Clark et al., 2001). These

models also need to be incorporated into easy-to-use tools for managers to test and compare

different management actions.

In this paper, we present the next-generation NOAA CRW coral disease forecasting

product (i.e., V3) that addresses some of these challenges and applies new, innovative

approaches to ecological forecasting. By integrating data from multiple sources and using

machine learning algorithms to identify patterns and make predictions, the system provides early

warnings of coral disease risk and helps managers and decision-makers take proactive measures

to protect reefs across much of the Pacific Ocean. This new Multi-Factor Coral Disease Risk

product expands the previous product in several ways through: 1) a broader geographic scope; 2)

consideration of two distinct groups of diseases; 3) inclusion of a suite of disease drivers; 4)

generation of weekly forecasts with a three-month lead time; 5) provision of measures of

uncertainty; 6) consideration of multiple scenarios; and 7) increased capacity for users to

visualize forecasts and modify scenarios through an interactive online dashboard used to explore

management strategies. The results of this study have broader implications for making

predictions in other complex, data-poor systems and highlight the need for continued research

and innovation in the field of ecological forecasting.

Methods

The Multi-Factor Coral Disease Risk product (i.e., V3) is an experimental regional

product, currently providing ecological forecasts for multiple locations in the Pacific Ocean.

Areas include American Samoa, Guam and the Commonwealth of the Northern Mariana Islands

(CNMI), Australia's Great Barrier Reef (GBR), Hawaii, and the U.S. Pacific Remote Islands

Marine National Monument (PRIMNM, also called the Pacific Remote Island Area, PRIA)

encompassing seven islands and atolls: Baker, Howland, and Jarvis Island; Johnston, Wake, and

Palmyra Atolls; and Kingman Reef. In this product, we assess disease risk based on satellite

remotely-sensed, modeled, and *in situ* data to provide nowcasts and near-term forecasts based on

current conditions, recent conditions, and subseasonal-to-seasonal forecasts from NOAA

operational climate models. We optimized the modeling system using a Pacific-wide dataset of

over 42,000 coral disease surveys (more detail below).

Data

We identified a suite of potential predictor variables to forecast coral disease risk based

on prior observational, experimental, and modeling efforts for two disease types (Tables 1, S1).

In this product, we forecast the risk of white syndromes and growth anomalies. White syndromes

refer to a suite of tissue loss diseases that cause coral mortality and range from acute to chronic

based on the speed at which the infection progresses (Bourne et al. 2015). Growth anomalies are

chronic diseases that persist at low levels year round and manifest as changes in skeletal

morphology, usually through increases in skeleton secretion and disorganization of corallites,

affecting colony growth and fecundity (Palmer and Baird 2018). The etiological agents of both

groups of diseases are unknown. Across a variety of host species, disease types, and regions,

some factors such as coral cover, coral colony size, and specific ranges of temperature have been

consistently associated with certain coral diseases, although the functional relationships may

differ slightly (Greene et al. 2020; Heron et al. 2010; Bruno et al. 2007; Ruiz-Moreno et al. 2012;

Caldwell et al. 2020). Thus, we considered appropriate derivations of these variables for all

diseases and regions, based on data availability. For instance, we considered accumulation of

anomalous temperatures for white syndromes because of statistical associations across multiple

large scale studies (Burke et al. 2023; Bruno et al. 2007; Heron et al. 2010; Maynard et al. 2011;

Howells et al. 2020), but focused on seasonal mean temperature for growth anomalies because it

has been experimentally associated with lesion development and growth (Stimson, 2011).

Additionally, there were several potential predictor variables that were unique to each disease

type, because the ecology of white syndromes and growth anomalies differ substantially. White

syndromes often exhibit strong seasonality due to ocean conditions, notably winter and

summertime thermal stress and changes in water quality (Haapkylä et al., 2011; Heron et al.,

2010; Maynard et al., 2011; Ruiz-Moreno et al., 2012). White syndromes have also been

associated with fish densities, but the effects are not consistent across studies and the underlying

hypothesis for this effect varies by fish functional group (Aeby, Williams, Franklin, Kenyon, et

al., 2011; Caldwell et al., 2020; Clemens & Brandt, 2015; Greene et al., 2020; Renzi et al., 2022;

Williams et al., 2010). Thus, we included available metrics of fish density for multiple fish types

and water quality (turbidity) in the white syndromes models. For growth anomalies, previous

studies indicate an association with low fish abundance, limited water motion, and poor water

quality via nutrient enrichment, coastal development, and proximity to dense human populations

(Aeby, Williams, Franklin, Haapkyla, et al., 2011; Caldwell et al., 2020; Yoshioka et al., 2016).

Therefore, we included metrics of fish populations, turbidity, and coastal development in the

growth anomalies models.

From a forecasting perspective, the predictor variables, or environmental conditions, that

we considered in this study can be roughly divided into three types based on their variability

through time: 1) time-invariant; 2) seasonally-changing; and 3) regularly-changing. We consider

time-invariant conditions as any predictor variable that does not change regularly through time,

or information about such change is unavailable or sparsely updated. We consider seasonally-

changing conditions as predictor variables that depend on time of year but are not date-specific.

Most of these variables have been developed in a way that represent repeated seasonal patterns

developed from multi-year datasets (i.e., climatologies). Finally, we consider regularly-changing

conditions as predictor variables that change, and can be measured and evaluated, over some

regular time interval. We used point estimate predictor variable data for model development

based on the time and location of coral disease surveys whereas we use gridded predictor

variable data for forecasts.

Time-invariant data

We collated time-invariant data from *in situ* surveys and remotely-sensed data. For each

predictor variable described below, which we used in at least one of the four region-by-disease

models, we provide further detail, including data sources and spatial resolution, in Table S1. To

characterize benthic cover, we used metrics of coral cover (0-100%), coral colony size, and

population level colony size variability (based on coefficient of variation). For these metrics, we

developed the models using data collected concurrently with coral disease surveys. We

aggregated these metrics by host family for the U.S. Pacific models and by morphology for the

GBR white syndromes models to be consistent with data collection methodology (more details

below). In the forecasts, we used a combination of survey data and gridded data from long-term

monitoring programs. For coral cover in the GBR and coral colony size in the U.S. Pacific, we

calculated pixel-specific mean values across the reef grid from long-term survey data (multiple

sources listed in Table S2) while for coral cover in the U.S. Pacific, we used sector level benthic

cover data from the NOAA National Coral Reef Monitoring Program (NCRMP). As fish surveys

were rarely conducted in coordination with benthic surveys, we used fish density layers from

long-term monitoring programs for both model development and forecasting. We used sector-

level fish data from NOAA NCRMP and ~2 km gridded fish count data based on manta tow

surveys from the Australian Institute of Marine Science (AIMS) Long Term Monitoring Program

(LTMP) (Sweatman HPA, Cheal AJ, Coleman GJ, E...). As a proxy for coastal development in

both model development and forecasting, we used NASA's Black Marble product, which is a

time-aggregated map of artificial light intensity (high gain) (0-255) at 3 km resolution from the

Visible Infrared Imaging Radiometer Suite (VIIRS) instrument aboard the Suomi-National Polar-

orbiting Partnership (NPP) satellite (Román et al., 2018). To characterize chronic water quality

conditions in both model development and forecasting, we aggregated the diffuse attenuation

coefficient at 490 nm, Kd(490), as a proxy for turbidity from VIIRS data (Kirk 1994). We

calculated long-term Kd(490) median and variability for each reef pixel by aggregating data

from 2012-2020 (i.e., all data available at time of study) within a 5-pixel buffer (750 m becomes

~8.25 km resolution) following methods from (Geiger et al., 2021) to increase data availability,

as nearshore ocean color data are notoriously patchy. These metrics are indicative of spatial

differences in water quality across reefs, providing information on locations that have

chronically good or poor water quality and those that are exposed to a large range of water

quality conditions throughout the year versus those with more consistent conditions.

Seasonally-changing data

We use month of year and two turbidity metrics to capture seasonally-changing

conditions that are relevant to disease risk. To characterize typical seasonal water quality

patterns, we calculated mean and variability of VIIRS-derived Kd(490) for a three-week moving

window across a 9-year time span (2012-2020) using the same 5-pixel buffer described above.

These metrics repeat annually and are indicative of how water quality changes throughout the

year in a given location. We used seasonal changes (climatology) in Kd(490) because, to date,

these values are too highly variable and too infrequently available in the coastal zone to use

actual, or even three-week, values. Additional details on the derivation of these metrics and their

accuracy can be found in (Geiger et al., 2021). We include month in the model as a proxy for all

other seasonally changing conditions.

Regularly-changing data

We include three temperature-based metrics in the disease models that update at regular

intervals: 90-day SST mean, Hot Snaps, and Winter Condition. In contrast to the seasonally-

changing data, the regularly changing data yield different values each year for the same time

period (e.g., the first week of January) based on observed and/or forecasted conditions. The daily

previous 90-day mean SST is the average daily SST values for the 90 days preceding the current

date. The Hot Snap and Winter Condition metrics were developed for NOAA CRW's Coral

Disease Outbreak Risk Product V1 and V2. The Hot Snap metric accumulates hot temperature

anomalies through time, relative to the locally/pixel-specific long-term expected summer

temperature (summer climatology) (Heron et al., 2010), providing an indication of exposure to

thermal stress. The Winter Condition metric accumulates both hot and cold temperature

anomalies during the winter season relative to locally-specific, long-term average temperature

(Heron et al., 2010), representing cold season variability. Mild winters have been linked to white

syndromes (Caldwell, Heron, et al., 2016; Heron et al., 2010), potentially because such

conditions allow pathogens to persist and grow throughout the winter season.

The data underlying these three temperature metrics differ for satellite observed

temperatures, which we used for model development and near real-time nowcasts, and forecasted

temperature, which we use for disease forecasts. For observed SST, we use CoralTemp v3.1

(Skirving et al., 2020), which provides daily data at a global resolution of ~5 km (0.05°). For

forecasted SST, we use output from the NOAA National Centers for Environmental Prediction's

operational Climate Forecast System Version 2 (CFSv2) (Saha et al., 2014). Each day, the

CFSv2 generates an ensemble of four SST forecasts out to 9 months at ~50 km (0.5°) resolution.

We use this output to form 28 ensemble member predictions each week (4 start times x 7 days)

for each predicted temperature metric and to predict the metric for three months following the

prediction date. The data are downscaled from ~50 km to ~5 km using a nearest neighbor

algorithm and then bias-corrected to match the 5 km satellite SST measurements during the

overlap between satellite observations and CFSv2 over the weekly time period when the 28

ensemble members are collected. Because predicted values demonstrate increased variability

with longer lead-times, SST anomaly values for the metrics are correspondingly adjusted to

match the variability of the SST data.

Coral Disease Survey Data

We assembled a Pacific-wide coral health monitoring dataset, which we used to develop

region- and disease-specific predictive models of disease risk. In total, we assembled over 42,000

coral health monitoring surveys between 2012 and 2020. Data came from the NOAA NCRMP,

University of Guam, Hawaii Coral Disease Database (Caldwell, Burns, et al., 2016), and the

Great Barrier Reef Marine Park Authority (GBRMPA; referred to as Reef Authority in other

contexts) Reef Health and Impact Surveys (Beeden et al., 2014). The different survey protocols

used to collect these data have been described in detail previously (Caldwell et al. 2016; Beeden

et al. 2014; Winston et al. 2020). For the research described in this paper, there are notable

methodological differences between surveys conducted in the U.S. Pacific and Australia;

therefore, we modeled disease risk in these two regions separately. Specifically, surveys in the

U.S. Pacific provided information to quantify family-specific disease prevalence (i.e., percent of

coral colonies affected by disease) while surveys from Australia indicated morphology-specific

disease density (i.e., number of diseased colonies in a given area); therefore the risk prediction is

for disease prevalence in the U.S. Pacific and disease density for Australia. While the U.S.

Pacific models are technically generated at the family level (Acroporidae for white syndromes

and Poritidae for growth anomalies), in practice, the data predominantly describe genus- or

species-specific patterns with various genera/species represented in different regions (Table S3).

We used these data to develop predictive models of elevated disease risk rather than outbreak

risk, which we believe is more appropriate as the data arise from regular monitoring surveys

rather than outbreak response surveys (outbreaks defined in Raymundo et al. 2008). If multiple

surveys were conducted in close proximity in time (i.e., in the same month) and space (the same

survey area), we randomly selected one of those surveys to keep in the dataset to avoid

artificially over-representing certain conditions.

Balancing data with SMOTE

To create disease models that produced reliable predictions of all levels of disease risk,

but particularly of high disease levels, we used a synthetic sampling technique to balance the

data used in model development. The observational surveys available to create the disease

models were highly unbalanced, with the majority of surveys reporting zero or low levels of

disease (Table S4); using unbalanced data would optimize disease-free predictions. Therefore,

we balanced the dataset before model creation using the Synthetic Minority Over-sampling

Technique (SMOTE; Chawla et al., 2002; Fig. 1a). We used the observed disease surveys with

their associated predictor variables to create additional synthetic disease surveys (using a k-

nearest neighbor algorithm) to produce a balanced dataset (e.g., approximately equal number of

disease and disease-free surveys with predictor variables). We created multiple SMOTE datasets

for each disease and region based on different disease level thresholds because it is unknown

whether the same environmental conditions that precede disease are responsible for low to high

levels of disease risk. In other words, we oversampled surveys with any disease and oversampled

surveys with greater than some specified level of disease and allowed the model selection

process to determine the best threshold to use. The disease level thresholds that we tested were 1,

5, and 10 colonies/75m^2 for white syndromes in the GBR and 1, 5, and 10% for white syndromes

in the U.S. Pacific; 1, 5, 10, and 15 colonies/75m^2 for growth anomalies in the GBR and 1, 5, 10,

15, and 20% for growth anomalies in the U.S. Pacific. These thresholds were chosen based on a

combination of natural breaks in the data and expert opinion. The threshold units align with the

survey data collected (i.e., density or prevalence) and therefore differ between the GBR and U.S.

Pacific. For each SMOTE dataset of disease surveys, we split the data into training and test data

using a 75/25 split. We used the training data for model creation and then the withheld test data

for model selection and assessment (described below).

Fig 1. Methodological overview for model development and weekly updating for each

disease-by-region model. (a.) Graphical illustration of Synthetic Minority Over-sampling

Technique (SMOTE) where the minority class (i.e., surveys with disease; large gray circles) are

used to create synthetic surveys of predictor and response data (i.e., small gray circles) based on

k-nearest neighbors (i.e., black lines connecting surveys in n-dimensional parameter space),

resulting in approximately equal numbers of surveys with (gray) and without (green) disease

present. In this study, we tested different thresholds for inclusion in the minority class. (b.) We

built the model using quantile regression forests, an algorithm that creates many decision trees

based on a subsample of predictor variables (example shows each tree using 2 of 3 possible

predictor variables), and produces a distribution of target values rather than a mean value. We

selected the most parsimonious model across the different SMOTE datasets and quantile

regression forests (i.e., with different combinations of predictor variables) based on a withheld

portion of the data, using the models with the fewest number of predictor variables with superior

predictive skill. The selected models are used in weekly updating for c-e. (c.) Each week, we

update predictor variables for the reef grid. Time-invariant predictor variables are held constant,

seasonal predictor variables update each week or month, near-real-time data reflect recent

satellite observations, and forecasted data come from 28-member ensemble CFSv2 SST

forecasts. (d.) Using the updated predictor data, we re-run the model to produce a new near real-

time prediction and 12 weeks of forecasted data, which we amend to the prior 11 weeks of

historical nowcast predictions for a total of six continuous months of disease risk assessments.

We also vary the predictor data across a gradient of values to produce scenarios, (e.) to explore

how disease risk changes with different input variable values.

Quantile regression forests

We created predictive models of disease risk using quantile regression forests

(Meinshausen, 2006; Fig. 1b). Quantile regression forests use a decision tree framework, allow

for non-linear relationships between response and predictor variables, and have shown high

predictive skill across a range of systems. Briefly, quantile regression forests are created by

developing an ensemble of quantile decision trees (i.e., random forests), with each tree created

from a bootstrapped resample of the dataset. Quantile decision trees differ from standard

decision trees in that they predict the distribution of target values rather than the mean target

value from the training data. This approach uses an ensemble of uncorrelated decision trees,

which tend to outperform any individual tree, and each tree uses a random subset of predictors to

increase variation among trees. The result of this process is that the final predictive model is

more robust because it is created from many trees that are trained on different subsets of

response data and predictor variables.

Model selection

We selected the most parsimonious model for each disease and region amongst a suite of

candidate models based on predictive skill on a withheld portion of the data. For each disease-

by-region pair, we ran a model that included all hypothesized predictor variables (Table 1) from

a training dataset (75% of surveys) and then used a backward selection approach to iteratively

remove predictor variables of least importance. Relative importance of each predictor variable

was calculated as the percent increase in Mean Squared Error (MSE) of out-of-bag cross-

validation predictions across permutations in that predictor variable, with higher values

indicating more important predictor variables. The exception was for the predictor variable

Month, which we retained in the model regardless of its relative importance because it captures

additional seasonal variation. At each model iteration, we predicted disease risk from a withheld

test dataset (25% of the surveys) and assessed predictive skill based on the R^2 value that arose

from linearly regressing those predictions with observations. We followed this approach of

backward selection for each SMOTE dataset. The selected (most parsimonious) model was the

model with the fewest predictor variables that produced an R^2 value within 1% of the best model

(i.e., highest R^2 overall).

Model assessment

To determine how well the models performed at retrospectively predicting disease levels

for each disease-by-region pair, we compared retrospective predictions by the models described

here with archived nowcasts from previous versions of the models where available (i.e., GBR

and Hawaiian archipelago) and how forecast skill changes with different lead times. For both

assessments, we quantified predictive skill using the withheld test data. To assess predictive skill

for white syndromes, we compared retrospective disease predictions from models described in

this paper (V3) with models supporting V2 using predictor data available from the week of

observations. The V3 models produce slightly different metrics of disease risk than the V2

models; therefore, we visually compared these results but did not directly compare their skill

quantitatively. Since there are no previous models in production for growth anomalies, we

assessed the retrospective model skill on the withheld test data alone. Additionally, we were

interested in whether and to what extent forecast prediction accuracy and precision changes as

we get closer to the observation date (i.e., shorter lead-times). To assess this relationship, we

predicted disease risk on the withheld data starting 12 weeks prior to each observation date (e.g.,

using SST forecasts available three months in advance of a survey) and made retrospective

predictions on the same observations at weekly intervals until the week of the observation (i.e.,

the nowcast). We calculated accuracy as the difference between the 75th quantile prediction and

the observation, resulting in zero if there was perfect accuracy, negative values if the models

predicted higher disease risk than observed, and positive values if the models predicted lower

disease risk than observed. We used the 75th quantile prediction (upper range of disease

likelihood) as the primary indicator of disease risk throughout this work, which was the metric

selected by the product end users to err on the side of potentially overpredicting disease in an

effort to further capture rare disease events. To assess predictive precision, we calculated the

difference between the 90th and 50th quantile predictions: larger differences indicate less precise

estimates and smaller differences indicate more precise estimates.

Weekly-updating predictions

The overarching objective of this research was to develop a product that provides

weekly-updating, near real-time, and subseasonal-to-seasonal disease risk forecasts. The

workflow for this process follows. First, we developed a reef location database based on a ~5 km

gridded reef locations dataset currently used by NOAA CRW (Heron et al. 2016) to set the

spatial extent of the disease outbreak forecasts described in this paper. This reef location

database encompasses all known shallow-water reefs within the U.S. Pacific Islands and atolls

and along the east coast of Australia, the majority of which fall within the GBR Marine Park. To

allow users to assess short-term temporal evolution of disease risk at each reef pixel, we provide

a moving window of six months of weekly predictions: the first three months with weekly

nowcast predictions based on observed environmental conditions (i.e., predictor variables

identified in the model selection process described above) up to the current calendar week, and

the second three months with weekly forecast predictions based on a combination of observed

(time-invariant data and seasonally-changing data) and forecasted environmental conditions. The

models and environmental conditions we use vary by disease and region, as described earlier and

in the Results section. For each week of predictions, we update the environmental input data

(Fig. 1c). The nowcast predictions (Fig. 1d) that we produce for each reef pixel are based on a

single set of observed environmental conditions and prediction uncertainty arises solely due to

model uncertainty. In contrast, we produce 28 forecast predictions for each reef pixel (Fig. 1d),

using 28 sets of SST-based metrics derived from the 28 different CFSv2 model runs, and thus,

uncertainty is composed of both model uncertainty and SST forecast uncertainty. In this product,

we chose to present predictions using the 50th, 75th, and 90th quantile predictions for the

reasons stated above (though any quantile(s) could be used). We also aggregate the risk

predictions to different management areas, which we collated from marine management

agencies. We do this by quantifying the 90th quantile values across all ~5 km reef pixels that fall

within the specified management area of the risk predictions (i.e., the 75th quantile modeled

risk). The use of the 90th quantile to spatially summarize risk predictions is consistent with other

regional summaries produced by CRW (Heron et al. 2016), with this value selected to alert users

to region-level risk whilst preventing potential exaggeration (e.g., by reporting the maximum

value across the region).

Weekly-updating scenarios

To allow users to customize the prediction to localized and current environmental

conditions and help determine the most appropriate intervention strategies, we also produce

weekly-updated scenario-based disease risk predictions (Fig. 1e). The predictions for various

scenarios show how adjusting current environmental conditions would change current disease

risk predictions. We calculate the change in disease risk by re-running the models iteratively,

varying a single environmental condition by specified amounts and holding all other location-

specific, current environmental conditions constant. The resulting scenarios allow users to 1)

refine predictions considering local conditions (e.g., a reef of interest) that may vary from the

mean conditions of the entire reef pixel or management zone; and 2) consider how an

intervention (e.g., a program to reduce turbidity) would affect disease risk. Following the format

we use to present near real-time and seasonal disease risk predictions, we also calculate changes

in disease risk for scenarios based on the 75th quantile disease predictions and aggregate the

results to management areas in the same way we describe earlier.

Results

Performance evaluation

The new Multi-Factor Coral Disease Risk product (V3) described in this study predicts

disease risk relatively well and qualitatively demonstrates superior predictive accuracy compared

with V2 for both the GBR and Hawaiian archipelago (Fig. 2). All versions have difficulty

predicting no or very low disease levels (i.e., below the selected SMOTE thresholds). V3 is the

first product to calculate uncertainty and can therefore represent this lack of predictability with

large uncertainty values, as shown around many low disease values. The major improvement can

be seen at mid- and high-levels of disease. While the previous algorithm predicts some high

disease events well, many are predicted to have no disease, suggesting that factors other than

thermal condition are key for predicting disease events.

Fig. 2 Accuracy of disease nowcast predictions demonstrate improved predictive capabilities for V3 compared with its predecessor. We show comparisons of disease observations (x-axes) with disease predictions (y-axes) for the current model (V3). Points that fall on the gray line indicate a perfect fit between observations and predictions. For white syndromes (left column), we compare disease predictions from V3 with V2 (note that predictions are only available for Hawaii in the U.S. Pacific). For growth anomalies, where no predecessor product exists, we show results for V3 only. V3 predicts disease density (colonies/75m^2) for the GBR (top row) and disease prevalence (percent of host colonies exhibiting signs of disease) for the entire U.S. Pacific (bottom row). The V3 product shows the 75th quantile predicted risk (points) and 50th - 90th quantile predictions (lines). The validation data shown in these plots were not used in model creation or training.

Lead time

Both accuracy and precision improved as lead time decreased, but not as drastically and

consistently as we expected (Fig. 3), indicating that as the survey date approaches the predictions

improve slightly. Positive values for accuracy indicate an over-prediction of disease in the

forecast (as shown for white syndromes on the GBR), whilst negative values indicate under-

prediction (growth anomalies in both regions). Accuracy improved with shorter lead time for

predictions in the GBR for both diseases, while there was almost no improvement with lead time

for predictions in the U.S. Pacific. In contrast, precision was largely unaffected by lead time,

with marginal improvements for white syndromes in the GBR and growth anomalies in the U.S.

Pacific. Given that the variability in SST forecasts decreased with decreasing lead time, these

results suggest that the prediction uncertainty is largely a function of model uncertainty rather

than SST forecast uncertainty.

Fig. 3. Lead time-dependent predictive accuracy and precision of forecasts. Barplots show

predictive accuracy (left column; calculated as difference between 75th quantile prediction and

observation) and predictive precision (right column; calculated as difference between 90th and

50th quantile predictions) with different lead times (0-12 weeks prior to observation date). In

these plots, perfect accuracy and precision are marked by horizontal dashed lines indicating zero

difference. Results are shown in eight panels for each of the paired disease types (white

syndromes and growth anomalies) and regions (GBR, Australia and U.S. Pacific). Predictions (y-

axes) calculated as disease density (colonies/75m^2) for the GBR and disease prevalence (percent

of host colonies exhibiting signs of disease ranging from 0-100%) for the U.S. Pacific. For

example, a median value of 10 for the GBR would indicate that, on average, the model predicts

10 more colonies as diseased than were observed. Similarly, a median value of -20 in the Pacific

would indicate that, on average, the model underpredicts disease prevalence by 20%. The

validation data shown in these plots were not used in model creation. Month, seasonal turbidity,

and SST metrics varied with lead time week, while all other predictor variables stayed the same

(e.g., benthic characteristics of site).

Coral disease drivers

The most influential disease drivers were primarily time-invariant or seasonally-changing

predictor variables (Table 1), which may explain why the V3 product predicts disease with

relatively high accuracy for observations from a range of locations and years (Fig. 2), but those

predictions do not change substantially with greater lead-time (Fig. 3). The most parsimonious

models for each disease-by-region pair varied slightly from each other but broadly reflected

relationships found in the literature (described in the Data section earlier; Figs. S1-4). Fish

density and winter condition were the best predictors of white syndromes in the GBR, followed

by variation in seasonal turbidity, summer thermal condition, and coral cover. For white

syndromes in the U.S. Pacific, median colony size and chronic and seasonal turbidity metrics

(both median and variability for each) were most important. Predictor variables for growth

anomalies in both regions were similar to each other, and included 90-day SST mean, fish

density, benthic cover metrics, and seasonal and chronic water quality. Within-site water quality

variability was more important for growth anomalies in the GBR, whereas average water quality

conditions along with coastal development were more important in the U.S. Pacific.

For distinguishing a gradient of disease risk across surveys, the model selection process

revealed that the predictor variables used are better suited for differentiating between lower and

higher levels of disease risk rather than presence-absence. We found that the models were able to

predict the gradient of observed disease risk best when oversampling surveys in the SMOTE

balancing process with relatively high levels of disease risk. For white syndromes, oversampling

surveys with >10 diseased colonies/75m^2 in the GBR and >10% disease prevalence in the U.S.

Pacific was optimal; for growth anomalies, oversampling surveys with >15 diseased

colonies/75m^2 in the GBR and >20% disease prevalence in the U.S. Pacific models was optimal

(Fig. S5).

Decision support tools

The experimental Multi-Factor Coral Disease Risk Forecast, a new tool within NOAA

CRW's decision support system for coral reef management, provides a regional ecological

nowcast and forecast of white syndromes and growth anomalies for multiple locations in the

Pacific Ocean. Via an online interface on the CRW website

(https://coralreefwatch.noaa.gov/product/disease_multifactor/index.php), users can access and

explore coral disease forecasts for their region of study, management, and/or interest in the

Pacific, to prepare for, monitor, and respond to coral disease outbreaks (Fig. S6).

Data explorer

To allow users to explore near real-time and seasonal disease predictions more closely,

we produced an interactive data explorer tool to complement the NOAA CRW Multi-Factor

Coral Disease Risk Forecast. The data explorer can be accessed through

https://coralreefwatch.noaa.gov/product/disease_multifactor/index.php or at

https://coraldisease.com. The data explorer has four components: 1) a disease risk page

visualizing nowcasts and forecasts across time and space (Fig. 4); 2) a scenarios page where

users can adjust environmental conditions to assess corresponding changes in the nowcast of

spatially-explicit disease risk; 3) a historical data page that provides information about survey

data used to build the models; and 4) an information page with explanatory information and

additional resources. Users can explore forecasts and scenarios at multiple spatial scales, ranging

from an individual ~5 km reef pixel to various management zones (containing multiple reef

pixels).

Fig 4. Data explorer for Multi-factor Coral Disease Risk product, accessed on 23 May 2022.

580　(A) Spatial view of overall color-coded disease risk nowcast for the Main Hawaiian Islands. (B)

581　Nowcast risk summary for geographic regions and diseases assessed. (C) Pixel-specific time-

582　series of nowcasted and forecasted risk on the south coast of Lanai (white arrow in panel A) for

583　growth anomalies and white syndromes, over a 5-month time period.

Discussion

The Multifactor Coral Disease Risk product (V3) offers many improvements over its

predecessors, providing a more holistic assessment of disease risk for reefs throughout the

Pacific Ocean, which has resulted in improved prediction capabilities. In addition to expanding

the geographic scope and types of diseases assessed, V3 provides weekly-updated nowcasts and

forecasts with up to three months of lead time. The predecessor products fundamentally differed

in their forecasting approach; V1 and V2 provide winter pre-conditioning risk outlooks at the end

of winter based on wintertime metrics derived from satellite remote sensing data, and then for

pixels that are pre-conditioned for risk, refined near real-time predictions are based on satellite

monitoring of Hot Snap accumulation throughout the summer months. Thus, within the summer,

these prior products produce nowcasts and do not make future predictions; the only prediction

component is for the following summer and only at the conclusion of a winter season based on

thermal conditions from the entire winter. Operationally, V3 requires constructing regular

predictions of SST-based metrics from climate models rather than relying entirely on near real-

time satellite remote sensing (as in V1 and V2). The three-month lead time in V3 aims to provide

local stakeholders with more time to organize and execute a response to potential outbreak

events. The accuracy and precision of forecast disease risk demonstrate a marginal level of bias

in applying the data-based model relationships with predicted values (Fig. 2), which may result

from variable skill in predicting the inputs (which here are the temperature-based metrics) rather

than in the model itself (see further discussion below). Through the online dashboard, users can

vary current or predetermined environmental conditions to refine disease risk predictions to

better reflect local conditions within the data grid and/or to assess impacts of potential

interventions. The most fundamental difference between V1/V2 and V3 is that the new product

assesses disease risk based on a suite of ecological conditions in combination with temperature

conditions, rather than temperature alone. Some of these new variables such as turbidity were

previously unavailable before the incorporation of VIIRS data into these models. Given the

relative importance of these new predictor variables (Table 1), we can conclude that although

suitable temperature conditions are necessary for elevated risk of white syndromes and growth

anomalies, other conditions like colony size and water quality are important driving factors. As a

result, the new models that consider a suite of conditions, aside from temperature, have

demonstrated better performance in retrospectively predicting disease risk in both the GBR and

U.S. Pacific.

While this analysis demonstrates that a suite of conditions are associated with white

syndromes and growth anomalies, challenges in forecasting these predictor conditions directly

limits capacity for disease prediction. The only predictor variables that are truly forecasted in the

Multi-Factor Coral Disease Risk product are the SST-based metrics. For all other variables, we

created seasonal climatologies, or rely on time-invariant layers based on long-term aggregated

data. For most of the time-invariant variables, such as coral cover, fish densities, and coastal

development, we do not expect conditions to change regularly. However, a single event can

drastically change biotic conditions on a reef (e.g., a mass bleaching event) and such changes

would not be reflected in the forecasts with the predetermined conditions, although they may be

assessed (at least to some degree) through adjusting scenarios based on updated information. We

foresee a similar issue for water quality metrics: while we expect that the seasonal climatologies

used in these models are fairly robust in the long-term, the current models do not capture acute

events caused by intense rainfall and associated runoff, which are known to influence disease

(Haapkylä et al., 2011). Although we attempted to measure acute events with ocean color data

(procedure described in Geiger et al., 2021), we found that the available data were too sparse to

use in the models, with no satellite coverage for ~80% of the corresponding survey data. More

importantly, the ocean color data unavailable during events were not random, but aggregated

during cloudy days; in other words, days that are most likely associated with rain events that can

increase disease risk. An alternative approach to forecasting water quality conditions could be to

create a model based on precipitation forecasts. However, precipitation forecasts are less skillful

than temperature forecasts and would require accurate prediction of the timing, intensity, and

location of rainfall at fine scales, which must be input into fine-scale hydrologic models with

accurate topography and well-predicted initial surface conditions (i.e., soil moisture). Such fine

scale hydrologic modeling is generally lacking for most tropical coasts. For this reason,

seasonally varying water quality climatologies are the most reliable measurements currently

available for coastal coral reefs. However, we see this process as analogous to early temperature

forecasts, which began as almanacs of past conditions (climatologies) and now show high

prediction skill through the deployment of increasingly sophisticated statistical and dynamical

models.

The extent to which temperature-based metrics are influential in the models determines

how well predictions reflect spatial versus temporal variability in disease risk. For white

syndromes on the GBR for example, both Winter Condition and Hot Snaps are relatively

influential variables. As a result, in the retrospective analysis, accuracy and precision varied

spatiotemporally – and improved with shorter lead times (consistent with the performance of

predicted temperature). In contrast, white syndromes in the U.S. Pacific are less strongly driven

by any of the temperature metrics tested in this study, and therefore variability in disease risk is

more apparent spatially than temporally. It is worthwhile to note that several white syndromes

outbreaks in the U.S. Pacific have occurred in winter (Williams et al. 2011; Aeby et al. 2016;

Caldwell et al. 2018; Greene et al. 2023); Greene unpublished), suggesting other factors may be

more important than temperature in this region or that some aspect of temperature not captured

by the metrics used in this study is important. For all disease-region pairs, but particularly those

with less reliance on temperature-based metrics, developing and/or improving climatologies and

forecast variables other than temperature would be the most effective way to improve

predictability within this forecasting system. A complementary and useful way of leveraging

information from V3 is to explore the spatial variability in disease risk to identify locations that

are most promising for interventions to improve reef health and target interventions to the most

influential variables. For instance, for white syndromes on the GBR, fish density and seasonal

turbidity variability were some of the most important predictor variables, indicating that

interventions directed at those factors may be most effective for improving reef health. From this

perspective, users can explore spatial variability in disease risk without concern over ephemeral

conditions that will elapse with weekly updating, and then track any intervention-associated

improvements through time.

Ecological forecasting presents a variety of ways scientists, managers, and decision-

makers can address the rising number of ecological challenges. We provide multiple pathways to

explore model predictions and suggest that major improvements going forward will be as

dependent on understanding the biological relationships as they are on additional monitoring and

surveillance data. The model outputs and associated online Multi-Factor Coral Disease Risk

product and data explorer were co-developed with relevant management agencies and scientists.

Through multiple focus groups with stakeholders in Australia, American Samoa, Hawaii, and

Guam, planning meetings, and workshop demonstrations at several scientific conferences over

the course of six years, we created an online decision support tool within the NOAA CRW

product suite that provides regional overviews aligned with other NOAA CRW tools with which

our intended audience is already familiar. The method of delivering regional overviews is also

preferred by users with slow or intermittent internet connection, as is common in some Pacific

islands. The data explorer complements this tool in several ways. First, it provides predictions

aggregated to relevant management zones and allows users to explore forecasts at these various

spatial scales through time. This addresses two key concerns of our users as they need to distill

information at scales relevant to their respective agencies or work mandates, and they wanted to

understand trends through time in those specific locations. We addressed a suite of other

concerns through the use of scenarios. Broadly, users, who interacted with the tools, as they were

being developed and tested, found it difficult to translate mean conditions at the finest spatial

scale (~5 km) to an individual reef of interest, especially when they knew conditions at that one

location were different from the surrounding region. Thus, we made it possible for users to

change individual input conditions in the scenarios page to see how predicted disease risk

changes in a specified area of interest. The same scenarios tool can alternatively be used as an

exercise to assess the predicted impacts of an intervention that would affect the input conditions

(e.g., an intervention to reduce resuspended sediments) to determine how that might affect

disease risk. Going forward, the forecasting models could be substantially improved by replacing

phenomenological relationships with biological ones. This would ideally be done using a

combination of lab and natural experiments and would ultimately help reduce uncertainty,

particularly for undersampled conditions. The overall modeling approach we used to create V3

could be replicated to predict disease risk for other reef regions and diseases, with appropriate

consideration given to the transferability of input variables to these systems. For example, Stony

Coral Tissue Loss Disease has caused widespread mortality in the Caribbean and Pacific coral

reef managers are extremely concerned about the potential for this disease to spread to the

Pacific basin; if it were introduced to the Pacific, V3 could be expanded to help forecast and

monitor its spread.

Many of the issues that make it challenging to forecast coral disease risk are issues that

encumber ecological forecasts more broadly. In many ecological systems, the greatest obstacle is

data limitation. For example, while we had extensive coral disease survey data that spanned a

large geographic range in the Pacific Ocean and a broad time horizon, very few of the data points

contained useful information about disease risk, as most surveys exhibited low or disease-free

conditions. This problem is likely to arise in other attempts to forecast low occurrence events

such as infestations, invasive species, tipping points, and extreme events. While the historical

low occurrence of disease is good ecologically, these data limitations inhibit both our ability to

develop initial ecological forecasts and to create a workflow with continual validation and

updates, which has been key to improving forecasts in other systems such as weather, storm, and

fire forecasting (Dietze et al., 2018). A complementary issue is the reliance on forecasted data as

inputs to an ecological forecasting model, which may have their own set of uncertainties and

challenges. An important question then arises from these shared obstacles across systems: is

there something inherently different and currently unknown about developing forecasts in

systems where data cannot be regularly updated and validated? Thus, this ecological forecast and

many others will benefit from community-wide progress in the field of ecological forecasting.

Conclusions

Herein, we present the next-generation NOAA CRW coral disease forecasting product

and an associated data explorer tool. It provides many advantages over its predecessors,

including near-term forecasts of coral disease risk in many major reefs in the Pacific Ocean. The

Multi-Factor Coral Disease Risk product predicts disease risk for white syndromes and growth

anomalies with greater precision and accuracy than previous products based on temperature

alone, and provides information for more diseases and regions. Co-developing the user interface

with the intended user base of scientists and managers resulted in a user-friendly online data

explorer tool that includes assessment of disease risk at different scales, quantification of

uncertainty in predictions, and the ability to adjust input conditions to assess effects on disease

outcomes. While this iteration is a major improvement to the NOAA CRW coral disease

forecasting products, largely thanks to numerous advances in the ecological forecasting

community and data availability, there are still numerous limitations for forecasting coral disease

risk. As data availability, forecasting capabilities, and our biological understanding of the system

improves, so can future versions of this product.

Acknowledgments: Sincere thanks to Maury Estes of the NASA Ecological Forecasting for

guidance and support throughout the project. Thanks also to the numerous people who provided

feedback during the development of the tools through formal workshops, user-engagement

meetings, and/or personal input. The scientific results and conclusions, as well as any views or

opinions expressed herein, are those of the authors and do not necessarily reflect the views of

NOAA or the Department of Commerce.

Funding: Version 3 (V3) product development was supported with funding from the NASA

Ecological Forecasting Program (Applied Sciences Program), through the University of Hawai'i-

Hawai'i Institute of Marine Biology, with support to NOAA Coral Reef Watch via Global

Science & Technology, Inc. It was conducted in close collaboration with James Cook University,

the University of Newcastle, and the University of New South Wales, through the multi-year

Fore-C project, "Forecasting Coral disease outbreaks across the tropical Pacific Ocean using

satellite-derived data". We thank the NOAA Coral Reef Conservation Program, which funds

Coral Reef Watch (CRW; CRCP Project #915) and the National Coral Reef Monitoring Program

(NCRMP project # 743; CRCPP); NCRMP was the source of the benthic and fish data in the

Pacific.

Conflicts of interest: On behalf of all authors, the corresponding author states that there is no

conflict of interest.

757
Literature Cited

Aeby, G. S., Callahan, S., Cox, E. F., Runyon, C., Smith, A., Stanton, F. G., Ushijima, B., &

Work, T. M. (2016). Emerging coral diseases in Kāne'ohe Bay, O'ahu, Hawai'i (USA): two

major disease outbreaks of acute Montipora white syndrome. *Diseases of Aquatic*

Organisms, *119*(3), 189–198.

Aeby, G. S., Williams, G. J., Franklin, E. C., Haapkyla, J., Harvell, C. D., Neale, S., Page, C. A.,

Raymundo, L., Vargas-Ángel, B., Willis, B. L., Work, T. M., & Davy, S. K. (2011). Growth

anomalies on the coral genera Acropora and Porites are strongly associated with host density

and human population size across the Indo-Pacific. *PloS One*, *6*(2), e16887.

Aeby, G. S., Williams, G. J., Franklin, E. C., Kenyon, J., Cox, E. F., Coles, S., & Work, T. M.

(2011). Patterns of coral disease across the Hawaiian archipelago: relating disease to

environment. *PloS One*, *6*(5), e20370.

Beeden, R. J., Turner, M. A., Dryden, J., Merida, F., Goudkamp, K., Malone, C., Marshall, P. A.,

Birtles, A., & Maynard, J. A. (2014). Rapid survey protocol that provides dynamic

information on reef condition to managers of the Great Barrier Reef. *Environmental*

Monitoring and Assessment, *186*(12), 8527–8540.

Bruno, J. F., Petes, L. E., Drew Harvell, C., & Hettinger, A. (2003). Nutrient enrichment can

increase the severity of coral diseases. *Ecology Letters*, *6*(12), 1056–1061.

Bruno, J. F., Selig, E. R., Casey, K. S., Page, C. A., Willis, B. L., Harvell, C. D., Sweatman, H.,

& Melendy, A. M. (2007). Thermal stress and coral cover as drivers of coral disease

outbreaks. *PLoS Biology*, *5*(6), e124.

Burke, S., Pottier, P., Lagisz, M., Macartney, E. L., Ainsworth, T., Drobniak, S. M., &

Nakagawa, S. (2023). The impact of rising temperatures on the prevalence of coral diseases

and its predictability: A global meta-analysis. *Ecology Letters*.

https://doi.org/10.1111/ele.14266

Caldwell, J. M., Aeby, G., Heron, S. F., & Donahue, M. J. (2020). Case-control design identifies

ecological drivers of endemic coral diseases. *Scientific Reports*, *10*(1), 2831.

Caldwell, J. M., Burns, J. H. R., Couch, C., Ross, M., Runyon, C., Takabayashi, M., Vargas-

Ángel, B., Walsh, W., Walton, M., White, D., Williams, G., & Heron, S. F. (2016).

Hawai□i Coral Disease database (HICORDIS): species-specific coral health data from

across the Hawaiian archipelago. *Data in Brief*, *8*, 1054–1058.

Caldwell, J. M., Donahue, M. J., & Harvell, C. D. (2018). Host size and proximity to diseased

neighbours drive the spread of a coral disease outbreak in Hawai'i. *Proceedings. Biological*

791  *Sciences / The Royal Society*, *285*(1870). https://doi.org/10.1098/rspb.2017.2265

792 Caldwell, J. M., Heron, S. F., Eakin, C. M., & Donahue, M. J. (2016). Satellite SST-Based Coral

793  Disease Outbreak Predictions for the Hawaiian Archipelago. *Remote Sensing*, *8*(2), 93.

794 Carlson, R. R., Foo, S. A., & Asner, G. P. (2019). Land Use Impacts on Coral Reef Health: A

795  Ridge-to-Reef Perspective. *Frontiers in Marine Science*, *6*.

796  https://doi.org/10.3389/fmars.2019.00562

797 Chawla, N. V., Bowyer, K. W., Hall, L. O., & Kegelmeyer, W. P. (2002). SMOTE: Synthetic

798  Minority Over-sampling Technique. *Journal of Artificial Intelligence Research*, *16*, 321–

799  357.

800 Clark, J. S., Carpenter, S. R., Barber, M., Collins, S., Dobson, A., Foley, J. A., Lodge, D. M.,

801  Pascual, M., Pielke, R., Jr, Pizer, W., Pringle, C., Reid, W. V., Rose, K. A., Sala, O.,

802  Schlesinger, W. H., Wall, D. H., & Wear, D. (2001). Ecological forecasts: an emerging

803  imperative. *Science*, *293*(5530), 657–660.

804 Clemens, E., & Brandt, M. E. (2015). Multiple mechanisms of transmission of the Caribbean

805  coral disease white plague. *Coral Reefs* , *34*(4), 1179–1188.

806 Dietze, M. C., Fox, A., Beck-Johnson, L. M., Betancourt, J. L., Hooten, M. B., Jarnevich, C. S.,

807  Keitt, T. H., Kenney, M. A., Laney, C. M., Larsen, L. G., Loescher, H. W., Lunch, C. K.,

808  Pijanowski, B. C., Randerson, J. T., Read, E. K., Tredennick, A. T., Vargas, R., Weathers,

809  K. C., & White, E. P. (2018). Iterative near-term ecological forecasting: Needs,

810  opportunities, and challenges. *Proceedings of the National Academy of Sciences of the*

811  *United States of America*, *115*(7), 1424–1432.

812 Geiger, E. F., Heron, S. F., Hernández, W. J., Caldwell, J. M., Falinski, K., Callender, T.,

813  Greene, A. L., Liu, G., De La Cour, J. L., Armstrong, R. A., Donahue, M. J., & Eakin, C. M.

(2021). Optimal Spatiotemporal Scales to Aggregate Satellite Ocean Color Data for

Nearshore Reefs and Tropical Coastal Waters: Two Case Studies. *Frontiers in Marine*

Science, *8*. https://doi.org/10.3389/fmars.2021.643302

Greene, A., Donahue, M. J., Caldwell, J. M., Heron, S. F., Geiger, E., & Raymundo, L. J. (2020).

Coral Disease Time Series Highlight Size-Dependent Risk and Other Drivers of White

Syndrome in a Multi-Species Model. *Frontiers in Marine Science*, *7*.

https://doi.org/10.3389/fmars.2020.601469

Haapkylä, J., Unsworth, R. K. F., Flavell, M., Bourne, D. G., Schaffelke, B., & Willis, B. L.

(2011). Seasonal rainfall and runoff promote coral disease on an inshore reef. *PloS One*,

6(2), e16893.

Heron, S. F., Willis, B. L., Skirving, W. J., Eakin, C. M., Page, C. A., & Miller, I. R. (2010).

Summer hot snaps and winter conditions: modelling white syndrome outbreaks on Great

Barrier Reef corals. *PloS One*, *5*(8), e12210.

Jordan, M. I., & Mitchell, T. M. (2015). Machine learning: Trends, perspectives, and prospects.

Science, *349*(6245), 255–260.

Maynard, J. A., Anthony, K. R. N., Harvell, C. D., Burgman, M. A., Beeden, R., Sweatman, H.,

Heron, S. F., Lamb, J. B., & Willis, B. L. (2011). Predicting outbreaks of a climate-driven

coral disease in the Great Barrier Reef. *Coral Reefs* , *30*(2), 485–495.

Meinshausen, N. (2006). *Quantile Regression Forests*.

https://www.jmlr.org/papers/volume7/meinshausen06a/meinshausen06a.pdf

Oliver, T. H., & Roy, D. B. (2015). The pitfalls of ecological forecasting. *Biological Journal of*

the Linnean Society. Linnean Society of London, *115*(3), 767–778.

Pollock, F. J., Lamb, J. B., Field, S. N., Heron, S. F., Schaffelke, B., Shedrawi, G., Bourne, D.

G., & Willis, B. L. (2014). Sediment and turbidity associated with offshore dredging

increase coral disease prevalence on nearby reefs. *PloS One*, *9*(7), e102498.

Renzi, J. J., Shaver, E. C., Burkepile, D. E., & Silliman, B. R. (2022). The role of predators in

coral disease dynamics. *Coral Reefs* , *41*(2), 405–422.

Román, M. O., Wang, Z., Sun, Q., Kalb, V., Miller, S. D., Molthan, A., Schultz, L., Bell, J.,

Stokes, E. C., Pandey, B., Seto, K. C., Hall, D., Oda, T., Wolfe, R. E., Lin, G., Golpayegani,

N., Devadiga, S., Davidson, C., Sarkar, S., … Masuoka, E. J. (2018). NASA's Black Marble

nighttime lights product suite. *Remote Sensing of Environment*, *210*, 113–143.

Rosales, S. M., Clark, A. S., Huebner, L. K., Ruzicka, R. R., & Muller, E. M. (2020).

Rhodobacterales and Rhizobiales Are Associated With Stony Coral Tissue Loss Disease and

Its Suspected Sources of Transmission. *Frontiers in Microbiology*, *11*, 681.

Ruiz-Moreno, D., Willis, B. L., Page, A. C., Weil, E., Cróquer, A., Vargas-Angel, B., Jordan-

Garza, A. G., Jordán-Dahlgren, E., Raymundo, L., & Harvell, C. D. (2012). Global coral

disease prevalence associated with sea temperature anomalies and local factors. *Diseases of*

Aquatic Organisms, *100*(3), 249–261.

Saha, S., Moorthi, S., Wu, X., Wang, J., Nadiga, S., Tripp, P., Behringer, D., Hou, Y.-T.,

Chuang, H.-Y., Iredell, M., Ek, M., Meng, J., Yang, R., Mendez, M. P., van den Dool, H.,

Zhang, Q., Wang, W., Chen, M., & Becker, E. (2014). The NCEP Climate Forecast System

Version 2. *Journal of Climate*, *27*(6), 2185–2208.

Selig, E. R., Drew Harvell, C., & Bruno, J. F. (2006). Analyzing the relationship between ocean

temperature anomalies and coral disease outbreaks at broad spatial scales. In *Coral Reefs*

and Climate Change: Science and Management.

Shore, A., & Caldwell, J. M. (2019). Modes of coral disease transmission: how do diseases

spread between individuals and among populations? *Marine Biology*, *166*(4), 45.

Skirving, W., Marsh, B., De La Cour, J., Liu, G., Harris, A., Maturi, E., Geiger, E., & Eakin, C.

M. (2020). CoralTemp and the Coral Reef Watch Coral Bleaching Heat Stress Product Suite

Version 3.1. *Remote Sensing*, *12*(23), 3856.

Stimson, J. (2011). Ecological characterization of coral growth anomalies on Porites compressa

in Hawai'i. *Coral Reefs* , *30*(1), 133–142.

Vega Thurber, R. L., Burkepile, D. E., Fuchs, C., Shantz, A. A., McMinds, R., & Zaneveld, J. R.

(2014). Chronic nutrient enrichment increases prevalence and severity of coral disease and

bleaching. *Global Change Biology*, *20*(2), 544–554.

Walton, C. J., Hayes, N. K., & Gilliam, D. S. (2018). Impacts of a Regional, Multi-Year, Multi-

Species Coral Disease Outbreak in Southeast Florida. *Frontiers in Marine Science*, *5*.

https://doi.org/10.3389/fmars.2018.00323

Williams, G. J., Aeby, G. S., Cowie, R. O. M., & Davy, S. K. (2010). Predictive modeling of

coral disease distribution within a reef system. *PloS One*, *5*(2), e9264.

Williams, G. J., Knapp, I. S., Work, T. M., & Conklin, E. J. (2011). Outbreak of Acropora white

syndrome following a mild bleaching event at Palmyra Atoll, Northern Line Islands, Central

Pacific. *Coral Reefs* , *30*(3), 621–621.

Yoshioka, R. M., Kim, C. J. S., Tracy, A. M., Most, R., & Harvell, C. D. (2016). Linking sewage

pollution and water quality to spatial patterns of Porites lobata growth anomalies in Puako,

Hawaii. *Marine Pollution Bulletin*, *104*(1-2), 313–321.

Table 1: Variable inclusion and importance differs for each disease-region model. Variable

importance indicates the order in which the predictor variables influence the model (1 = most

influential). The variables tested and selected, as well as their importance, differ for each region

(Great Barrier Reef or U.S. Pacific) and disease type (white syndrome or growth anomalies). A

cell with a value indicates that the variable was selected for the model and the value represents

the percent increase in Mean Squared Error (MSE) of out-of-bag cross-validation predictions

across permutations in that predictor variable, with higher values indicating more important

predictor variables. (Note that MSE is sensitive to units even though the percent increase in MSE

is unitless; thus values for the GBR models that predict disease density will typically be much

larger than values for the U.S. Pacific models that predict disease prevalence). ☐ indicates a

variable was tested but not selected; a blank cell indicates that the variable was not tested for that

model because it is not a hypothesized predictor variable whereas Ø indicates that a variable was

not tested because data were not available. Metrics that measure Kd(490) are a proxy for

turbidity.

Variable importance (1 = most, 10 = least)									
1	2	3	4	5	6	7	8	9	10

Predictor variable	White syndromes		Growth anomalies	
	GBR	U.S. Pac	GBR	U.S. Pac
Time-invariant predictors				
Coral cover	51	0.8	487	☐
Median colony size	Ø	2.3	Ø	5.3
Colony size variability			Ø	☐
Herbivorous fish density	68	1.2	641	2.3
Parrotfish density	Ø	0.6		

Butterflyfish density	∅	☐		
Long term Kd(490) median	☐	2.2	☐	1.9
Long term Kd(490) variability	☐	1.9	399	☐
Coastal development			☐	3.1
Seasonally-changing predictors				
Three-week Kd(490) median	☐	1.3	350	1.8
Three-week Kd(490) variability	59	1.7	345	☐
Month	37	1.1	310	2.5
Regularly-changing predictors				
90-day SST mean			413	5.6
Hot Snaps	53	☐		
Winter Condition	62	0.8		

897
898