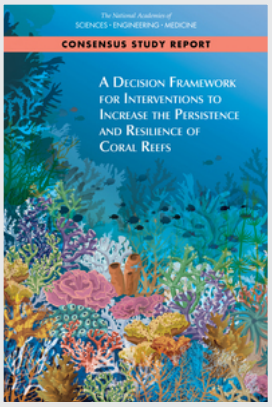

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A Decision Framework for Interventions to Increase the Persistence and Resilience of Coral Reefs

Committee on Interventions to Increase the Resilience of Coral Reefs

Ocean Studies Board

Board on Life Sciences

Division on Earth and Life Studies

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This Consensus Study Report was reviewed in draft form by individuals chosen for their diverse perspectives and technical expertise. The purpose of this independent review is to provide candid and critical comments that will assist the National Academies of Sciences, Engineering, and Medicine in making each published report as sound as possible and to ensure that it meets the institutional standards for quality, objectivity, evidence, and responsiveness to the study charge. The review comments and draft manuscript remain confidential to protect the integrity of the deliberative process.

We thank the following individuals for their review of this report:

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Although the reviewers listed above provided many constructive comments and suggestions, they were not asked to endorse the conclusions or recommendations of this report nor did they see the final draft before its release. The review of this report was overseen by **David Karl**, University of Hawaii at Manoa and **Holly Greening**, CoastWise Partners. They were responsible for making certain that an independent examination of this report was carried out in accordance with the standards of the National Academies and that all review comments were carefully considered. Responsibility for the final content rests entirely with the authoring Committee and the National Academies.

Preface

Ecosystems around the world face increasing stress from human populations, and this is just as true in the oceans as on land. Coral reefs in particular are damaged by a wide range of factors, including overfishing, sediment, pollution, and habitat destruction. Added to these local stresses are a new range of deleterious impacts from climate change, which increases ocean temperature, storm damage, ocean acidity, and sea level. Because coral reefs directly provide food, living area, storm protection, and tourism income to hundreds of millions of people, maintaining their stability in the face of local and climate stressors is a key goal for supporting human well-being around the world.

We are not powerless to slow the decay of coral ecosystems in the face of climate change. But any successful effort requires careful application of a range of management tools at a regional scale, which needs time, effort, and often international cooperation. The Committee on Interventions to Increase the Resilience of Coral Reefs was asked to review the state of research on methods that have been used, tested, or proposed to increase the resilience of coral reefs. In our first report, we described and summarized 23 different interventions in four broad categories. The interventions differ widely in readiness and none are ready to be used at a global scale. In all cases, use of any of these interventions demands simultaneous efforts to reduce local stressors and reduce the impact of global greenhouse gas emissions on the world's climate.

To navigate the sets of management choices that these many interventions provide, the committee turned to current methods of making complex management decisions when there are many possible avenues of action. In this report, we follow the best practices for decision analysis, emphasizing the need for community involvement and detailed modeling in goal setting and risk analysis. The committee strived to lay out a framework that includes a range of methods for evaluating interventions, while emphasizing the primary role of localized goals and preferences based on local environmental monitoring. The Caribbean is a notably stressed region, depauperate of corals and plagued by disease, and provided the committee with a key case study for directing the use of a decision framework.

The group that together accomplished this effort—from the members of the committee to many levels of National Academies of Sciences, Engineering, and Medicine staff—dedicated themselves to a long journey through many different kinds of information and many different ways of thinking, from genomics to decision science. Throughout, it has been a pleasure to work with, and sometimes just sit back and watch, the dedicated action, attention to detail, commitment to deadlines, and creativity of this thoughtful group. A sense of common resolve—that the world we live in, especially the beautiful reefs that we love, needs a different kind of immediate help—has pervaded our efforts. Last, our National Academies staff leaders Emily Twigg and Andrea Hodgson could not have been more effective at facilitating the balance between the practical and the audacious, which is the pivot point on which efforts to sustain all of Earth's ecosystems balances.

Stephen Palumbi, Chair
Committee on Interventions to Increase the Resilience of Coral Reefs

Contents

Summary

Coral reef managers are faced with a new decision crisis: deteriorating environmental conditions are reducing the health and functioning of coral reef ecosystems worldwide. Recent episodes of sustained above-average water temperatures have increased the frequency of coral bleaching events and are associated with increased disease outbreaks. Carbon dioxide dissolution in the ocean is lowering the pH of seawater, which is slowly impairing the ability of corals to grow or maintain their skeletons via calcification. These growing threats compound the persistent local stresses coral reefs have experienced for decades from pollution, overfishing, and habitat destruction. A growing body of research on "coral interventions" aims to increase the ability of coral reefs to persist in these rapidly degrading environmental conditions. These new tools are needed because established approaches for managing coral reefs are neither sufficient, nor designed, to preserve corals in a changing climate. Coral interventions that address the impacts of ocean warming and ocean acidification are part of a three-pronged approach for coral reef management that crucially also includes the mitigation of greenhouse gas emissions and the alleviation of local stressors.

New coral interventions include activities that affect the genetics, reproduction, physiology, ecology, or local environment of corals or coral populations with the goal of enhancing their persistence and resilience in degraded environmental conditions. They build on a growing understanding of how the coral holobiont—the coral, its symbiotic algae, and the rest of its microbiome—responds, acclimatizes, and adapts to stress. Ultimately, the goal of the interventions is to alter the reef in some way, by shifting population structures, altering genes, or changing the composition of symbiont and microbiome communities. These changes may benefit coral reefs, the species that live on them, and the human communities that depend on them. But these changes provide very different benefits across sites and may have unintended consequences that will similarly vary across locations.

An ad hoc committee was convened by the National Academies of Sciences, Engineering, and Medicine to evaluate the potential for these new interventions to increase the persistence and resilience of coral reefs, and to provide a framework for evaluating their risks and benefits. In their first report (NASEM, 2019), the committee reviewed the state of science on potential interventions. The report addresses what is known about the benefits and goals, current feasibility, potential scale, risks, limitations, and infrastructure needs for 23 novel approaches. The committee's tasks for this second report were to (1) provide a framework for assessing relative risks and benefits of interventions, including in comparison to a baseline or no action; (2) describe a decision pathway that spans the range of actions from new research to future implementation; (3) identify research needs that would refine the intervention strategies and reduce critical uncertainties in the environmental risk assessments; and (4) assess the potential for interventions to meet management objectives for Atlantic/Caribbean coral reefs (the full task can be found in Box 1.1). This study was requested and funded by the National Oceanic and Atmospheric Administration, with additional support from the Paul G. Allen Family Foundation.

Best practices for decision making rely on a reef-specific, structured approach that includes input from relevant stakeholders to develop objectives and identify preferred options and decision

criteria, as well as detailed modeling of the coral ecosystem and how it affects ecosystem services. Community involvement happens early on in the process, and because obtaining this input for any specific location was outside the tasks set for the committee, the committee could not provide specific decision analyses for any local reef system. Instead, the report provides a set of guidelines and principles that incorporate best practices for informing decisions under uncertainty when evaluating new interventions, including an example analysis to illustrate the use of such a framework.

In this report, the committee first reviews the interventions from the first report to assess their practical readiness and context dependencies to illuminate how managers may select interventions most suited to their situation for further assessment in a decision framework (Chapter 2). Next, the committee describes best practices for structured decision making, including evaluating risks and benefits, for taking an intervention from research to inclusion in a management strategy, and the available tools that have been, or might be, applied to coral reef management (Chapter 3). The committee provides an illustrative model and decision analysis of a coral reef system to exemplify the challenges and insights associated with decision making around coral interventions (Chapter 4). The committee then highlights research areas that would help inform decision making by improving the understanding of the baseline reef system, assessing risks, and managing the beneficial impacts of potential interventions (Chapter 5). Finally, the committee uses the Atlantic/Caribbean region as a case study for how managers may consider their individual context and objectives in an evaluation of possible intervention strategies (Chapter 6).

SELECTING INTERVENTIONS FOR DECISION ANALYSIS

Managers and decision makers are faced with the task of evaluating the benefits and risks of a growing number of interventions, separately and in combination. A number of factors helps narrow down the field of options. Primarily, readiness or the timeframe for achieving readiness for implementation will determine which interventions are practical on short- or long-term timeframes. For example, testing corals for heat resistance and growing them in nurseries is available to support managed selection, managed breeding, and managed relocation. In contrast, using genetic engineering to increase resilience, or marine cloud brightening to reduce light and cool reef surface waters are not yet feasible, and the risks and benefits of these are not well defined. Interventions available immediately can buy time until more, and potentially more impactful, interventions can become ready for use, or until greenhouse gas emissions are reduced or removed and warming is abated.

The interventions have different risks, benefits, and feasibilities in different regions. Biophysical attributes of a reef or region that influence the choice of intervention include the current degree of reef degradation, disease prevalence, bleaching history and future projections of bleaching events, water quality, herbivory, recruitment, connectivity, spatial extent of the reef, potential for cold shocks, and temperature variability. Moreover, these dependencies are likely to differ when considering where to test versus where to deploy or scale up interventions. Existing management programs and infrastructure will also influence which interventions are more readily deployed. These existing programs and resources will include restoration programs based on sexual

reproduction (for genetic and reproductive interventions), technical expertise and research infrastructure availability (for various physiological interventions), propagation programs (for population and community level interventions), and significant engineering infrastructure and scalability (for environmental interventions). The process of identifying appropriate interventions, as well as the locations best suited for their implementation, will likely require coordination across management entities that may be multijurisdictional or multinational in nature. Furthermore, there may be efficiencies that can be found across interventions that share biological or infrastructural resources and can be implemented in combination.

Conclusion: Multiple, inter-related interventions provide a toolbox for increasing coral reef persistence and resilience. This set of options can be tested and deployed based on community goals, ecological objectives for reef management, and the benefits and risks across multijurisdictional or even multinational boundaries. These efforts are likely to evolve over time as interventions become more feasible and as new interventions are developed.

A STRUCTURED, ADAPTIVE APPROACH TO DECISION MAKING

Coral reefs are social-ecological systems; humans are responsible for the greatest threats to reef persistence and resilience yet are also among the primary beneficiaries of healthy and functional coral reefs that provide a variety of ecosystem services and benefit streams. A structured decision approach for managing coral reefs links driving forces, human and natural pressures, ecosystem states, measured impacts on ecosystem services, and societal and management responses in a coral reef system. The evaluation of coral interventions is part of a broader decision context that includes managing other stressors (e.g., water quality, overfishing, habitat destruction) to achieve overall coral reef conservation objectives based on community values. Within this framework, an adaptive management approach provides an explicit process for planning, evaluating, implementing, monitoring, and adjusting specific management strategies (e.g., interventions, conventional restoration activities, and their timing) when outcomes are uncertain, based on their measured impact and the overall management goals. The steps of this adaptive process, focused on evaluating coral interventions, are outlined below.

Step 1: Identify the decision context

An iterative adaptive management process begins with a planning and problem formulation stage to establish the decision context: identifying long- and short-term goals, objectives, possible biophysical outcomes, and their relationship to evaluation metrics and decision criteria. Although decision makers have primary responsibility for problem formulation, stakeholder involvement is required to establish shared goals and objectives. Stakeholders may have multiple and sometimes conflicting viewpoints, and also have varying risk tolerances to management alternatives (both unintended and known potential negative consequences). The process of reaching consensus on objectives and criteria will make preferences and risk tolerance explicit and will help guide how some objectives might need to trade off with others given stakeholder and decision maker values.

Step 2: Model linkages across interventions, biophysical outcomes, and objectives

Evaluation of expected intervention risks and benefits requires modeling, as quantitatively as possible, the biophysical (and, as appropriate, social and economic) consequences of implementing different interventions or set of interventions. Model design and input parameters should be tailored to specific locations at relevant spatial and temporal scales. Biophysical models assume that coral reef systems are naturally highly dynamic and characterized by stochastic variability, and that there is uncertainty in knowledge of these dynamics. Model outputs for reef condition can include attributes such as coral growth, reproductive capacity, coral cover, coral diversity, herbivore biomass, coral disease, macroalgae cover, and other metrics identified by researchers and stakeholders as critical indicators of coral reef health and resilience. To assess the consequences of interventions (or inaction) for society, metrics of coral reef health are mapped directly to agreed-upon decision criteria that translate to impacts on ecosystem services, representing the economic, social, and cultural values of stakeholders and decision makers.

Step 3: Analyze tradeoffs in criteria across alternatives

Reef managers are likely to consider a range of management alternatives, including using one or more interventions in concert with conventional restoration activities as well as taking no action. These combinations, along with uncertainty in knowledge about the reef system and future environment, will yield a range of modeled outcomes across alternatives with tradeoffs in their abilities to meet management objectives and minimize risk. For example, some intervention strategies may support the growth of a small subset of coral species that provide fish habitat but not the solid reef structure that is needed to provide coastal protection from storm waves. If fish habitat and strong reef structure are both key objectives for different stakeholder groups, then tradeoffs need to be made to reconcile different priorities or value preferences. A number of tools are available for analyzing these tradeoffs to guide a preferred course of action. These include multi-criteria decision analysis, decision trees, system dynamics models, and Bayesian networks. Most importantly, analyzing tradeoffs requires a deliberative approach with stakeholder values at the center.

Step 4: Select interventions or combination of management activities and determine evaluation metrics

Once decision-makers understand the potential performance of the suite of intervention strategies relative to the multiple objectives, and tradeoff analyses have generated an agreed subset of preferred strategies, one or more strategies can be selected for implementation. Measurable evaluation metrics are developed across decision criteria that link to the objectives established in Step 1 and are used to iteratively evaluate whether objectives are being achieved. For example, a decision criterion might be to increase coral cover and diversity to create fish habitat. The associated evaluation metrics might then be abundance and diversity of coral and fish species measured at appropriate time intervals.

Steps 5 and 6: Implement interventions, and initiate and sustain a monitoring plan

A targeted monitoring program, conducted prior to, during, and after implementation that is based on specific biophysical outcomes, is needed to provide the data necessary to quantify the evaluation metrics. Effective and targeted monitoring is critical to assess intervention performance compared to objectives, and to reduce critical uncertainty in models.

Steps 7, 8, and 9: Evaluate, communicate, and adapt
Evaluation of monitoring data can identify progress made toward meeting management objectives (including partial success or failure), or reveal the need for more information. The results of the evaluation can be used to communicate progress in meeting objectives to stakeholders and decision makers. The adaptive management framework allows for monitoring data to inform iterative improvements to model design and input parameters to inform strategy adjustment.

Conclusion: Although many tools exist for structured decision making to evaluate interventions as part of a reef management strategy, there is no single generalizable approach and no substitute for working through a structured decision process with stakeholders in the local context. This effort provides a data- and values-informed basis for selecting and evaluating management options against a set of objectives.

Recommendation: A structured adaptive management framework that considers all drivers and pressures affecting coral reefs should be developed to evaluate tradeoffs across alternatives and identify when and where new coral intervention(s) will be beneficial or necessary. This framework should include:

- **Engagement of a broad set of stakeholders to establish objectives and courses of action that reflect community values.**
- **Development of models tailored to the local environmental and ecological setting, management objectives, and preferred intervention options.**
- **Targeted monitoring of short- and long-term metrics of reef health and resilience.**
- **Iterative evaluation and adjustment of management strategies.**

AN ILLUSTRATIVE DECISION MODEL

The committee provides a simple model and Bayesian network analysis to illustrate the principles of a decision analysis for a simplified reef system, and the potential questions faced and insights gained from the approach. Though the results of the analysis are not reef-specific, the illustration provides a concrete example of the construction of a decision support framework to analyze the risks and benefits of example interventions, evaluate the likelihood of achieving intervention goals under different scenarios, and communicate potential outcomes. The example focuses on a subset of interventions through which a range of benefits and risks of intervention can be illustrated: assisted gene flow and atmospheric shading (i.e., marine cloud brightening). In practice, a more extensive set of interventions and their combinations would be explored in a localized context. The potential for these example interventions to support reef persistence under climate change was also analyzed in combination with the management of local stressors to demonstrate the relative importance of continuing these practices along with adopting new strategies.

Biophysical Model

The committee constructed a biophysical coral community model to capture the basic ecological dynamics of the reef system (Figure S.1). The committee used a simple model appropriate for

qualitative, comparative interpretation; any model constructed for a decision-making process would use a more realistic and locally-tailored modeling framework appropriate for more quantitatively precise predictions. As a proxy for a range of coral responses and community states, the model predicts the proportion of area covered by macroalgae and two types of coral: slow-growing coral (such as a foliose or massive coral) and fast-growing coral (such as a branching coral). Dynamics of growth, baseline mortality, and competition are modeled as continuous processes; bleaching and recruitment are modeled as discrete events. The model builds on the approach presented in Mumby et al. (2007), which has been adapted by others.

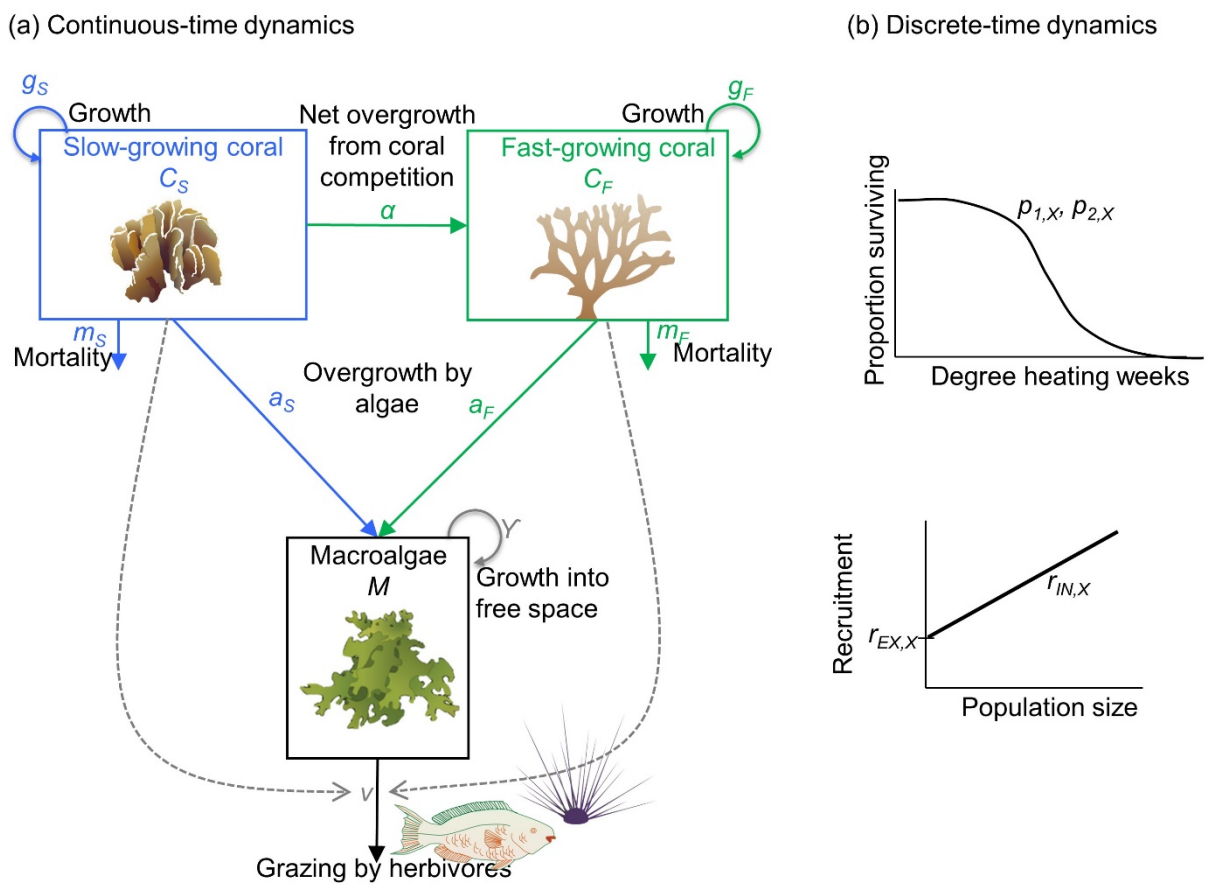


Figure S.1 Conceptual diagram of the simple coral-macroalgae community model. (a) Continuous-time dynamics, where boxes identify the populations that change over time (slow-growing corals, fast-growing corals, and macroalgae) and arrows indicate processes determining continuous dynamics (competition, growth [lateral extension], and mortality) and their directionality of impact. Dashed lines indicate the influence of coral cover on grazing rate by herbivores. (b) Discrete-time dynamics, with survival from bleaching dependent on the amount of thermal stress (measured as degree heating weeks) and both internal and external recruitment.

The proportion of mortality due to bleaching is modeled as a function of predicted degree heating weeks (DHW) based on global climate model projections. The committee includes estimates of how natural adaptation by corals, whether through acclimatization and/or genetic adaptation, might keep up with predicted increases in thermal stress associated with climate change. The committee represents the potential for natural adaptation using variable windows for

rolling climatologies as presented in Logan et al. (2014), in which adaptation or acclimatization occurs as the corals' threshold for experiencing thermal stress (DHW) changes based on recent thermal history. Accounting for natural adaptive processes enables better identification of situations where interventions will be needed, and also allows for a process to represent the benefit of interventions that accelerate adaptation.

Modeling Benefits and Risks of Interventions

Model evaluation of interventions requires representation of both risks and benefits in the model parameters. Table S.1 identifies how the risks and benefits of each intervention may be modeled using the committee's example framework. However, different modeling frameworks will offer more detailed mechanistic representation across risks and benefits for necessary predictive power. For example, while using a rolling climatology window calculation of DHWs implicitly accounts for adaptation or acclimatization processes, explicitly accounting for genetic dynamics could allow a model to predict the expected evolutionary outcome from interventions that affect genetic composition rather than assuming a particular adaptation rate.

For the example interventions, assisted gene flow occurs as an accelerated adaptation in thermal tolerance with the risks of increased mortality and decreased growth (due to outbreeding depression, demographic tradeoffs with thermal tolerance, and disease introduction), and shading occurs as reduced DHW exposure, with a risk of slowed adaptation in thermal tolerance and occasional shading failure. In addition, the committee also considered two other scenarios: (1) no intervention (a baseline of no action), and (2) applying conventional management strategies by varying herbivory rate (v; influenced by management of overfishing) and macroalgal growth rate (γ; influenced by control of nutrient runoff), alone or in combination with these interventions. The committee also explored a range of values for initial coral cover (5% vs. 30%), climate scenarios based on the IPCC's representative concentration pathways (RCP 2.6 vs. 8.5), and intervention start dates (2025 vs. 2035), with decadal target dates for assessing the coral cover outcome (2020-2060).

Bayesian Network Analysis

Simulation of all intervention strategy options, over a range of conditions and time, along with environmental stochasticity in DHWs results in a distribution of possible outcomes for total coral cover, the model's focal evaluation metric. The committee demonstrates the use of Bayesian network analysis to convert the range of outputs from the dynamic model to a network of conditional probabilities to inform decision making. That is, it shows how one condition (e.g., achieving coral cover of at least 20%) depends on the probability of other conditions being met and which conditions matter the most (e.g., the implementation of an intervention versus strong climate mitigation). Figure S.2 illustrates the probabilities of achieving at least 20% coral cover compared across the various management strategies and contrasting climate scenarios. Example conclusions that decision-makers might draw from an analysis of this type include: (1) intervention risks outweigh benefits under strong climate mitigation (RCP 2.6), but benefits outweigh risks for business-as-usual emissions (RCP 8.5), and (2) under business-as-usual climate change, intervention success relies on effective local management. These conclusions will vary with context-dependent model development, parameterization, and ground-truthing.

Table S.1 Anticipated benefits and risks of interventions and the biophysical parameters for modeling using the committee's example model

	Relevant interventions	**Potential effect in committee's model**	**Relevant mechanistic modeling framework**
BENEFIT			
Increase thermal tolerance physiologically	Pre-exposure, algal symbiont manipulation, microbiome manipulation, antioxidants, and nutritional supplementation	Temporarily increase coral survival at a given DHW (lowering $p_{2,X}$ in $h_X(\tau)$)	Physiological model
Increase thermal tolerance via genetic adaptation	Managed selection, managed breeding, genetic manipulation, assisted gene flow	Narrow rolling window for calculating the DHW value in $h_X(\tau)$	Genetic model
Reduce exposure to thermal stress	Shading, mixing of cool water	Reduce DHW experienced	Oceanographic model
Reduce exposure to OA stress	Abiotic OA interventions, seagrass meadows and macroalgal beds	Incorporate OA-dependency for coral growth (g_X)	Structured population model
Increase disease tolerance	Antibiotics, phage therapy, microbiome manipulation	Decrease coral background mortality (m_X)	Disease dynamics model
Enhance population size	Managed breeding, gamete and larval capture and seeding, managed relocation	Increase in coral external recruitment ($r_{EX,X}$)	Structured population model and genetic model
RISK			
Reduced fitness (e.g. outbreeding depression, domestication)	Managed breeding	Increase coral background mortality (m_X)	Genetic model
Reduced rate of adaptation	Shading, mixing of cool water, abiotic OA interventions, seagrass meadows and macroalgal beds	Widen rolling window for DHW value in $h_X(\tau)$	Genetic model
Tradeoff between stress tolerance and other demographic processes	Managed selection, assisted gene flow, antioxidants, algal symbiont or microbiome manipulation, pre-exposure, OA interventions	Decrease coral growth (g_X) and/or increase coral background mortality (m_X)	Physiological model
Disease or other pest introduction	Managed relocation	Increase coral background mortality (m_X)	Disease dynamics model
Destabilization of beneficial versus deleterious microbes	Microbiome manipulation, antibiotics, phage therapy	Increase coral background mortality (m_X)	Physiological model
Increased macroalgal growth	Nutritional supplementation, macroalgal beds to reduce OA	Increase in algal growth (γ)	Community model with explicit herbivore dynamics

Year	Scenario	StartState	DeployYear	A: No management	B: Best-Practice Management (BPM)	C: BPM + High AGF	D: BPM + AGF + Shading	E: AGF + Shading
2040	RCP 2.6	Low	2025	8	12	29	30	8
2040	RCP 2.6	High	2025	8	17	50	42	13
2040	RCP 8.5	Low	2025	8	21	36	33	8
2040	RCP 8.5	High	2025	8	13	59	38	8
2060	RCP 2.6	Low	2025	8	92	58	83	8
2060	RCP 2.6	Low	2035	8	92	83	75	8
2060	RCP 2.6	High	2025	8	92	67	75	8
2060	RCP 2.6	High	2035	8	92	83	83	8
2060	RCP 8.5	Low	2025	8	8	42	17	8
2060	RCP 8.5	Low	2035	8	8	58	42	8
2060	RCP 8.5	High	2025	8	8	50	25	8
2060	RCP 8.5	High	2035	8	8	58	17	8

Figure S.2 Results of the example Bayesian network analysis, identifying percent likelihoods (red to green scaled boxes) that a management strategy (options A to E) sustains coral cover above 20% over a variety of conditions (blue boxes). A: No intervention or change in management. B: Best practice management includes local stressor and fishing pressure control. C: Assisted gene flow (AGF) is added to best practices. D: Reef shading is added to 'C'. E: Reef shading and assisted gene flow are used without management of local stressors.

Conclusion: A successful modeling framework requires substantial effort in tailoring model structure and parameters to the decision context, risks, and benefits of the interventions under consideration, and local environmental conditions and reef ecosystem dynamics. As demonstrated by the committee's illustrative effort, the utility and payoff of this approach is the ability to identify

- **The conditions necessary for new and potentially risky interventions to outperform the no-action alternative under different future climate scenarios.**
- **The interventions expected to be most effective at achieving management objectives.**
- **Potential synergistic and antagonistic interactions across multiple interventions, including management of local stressors.**
- **The key dynamics and parameters to resolve empirically in order to improve the capacity to predict intervention efficacy and risks.**

Further applications of such modeling frameworks include identifying indicators for context- or condition-dependent decisions, monitoring, and adaptive management. The insight provided by a quantitative model enables decision makers and reef stakeholders to compare the benefits and risks of different intervention options with more clarity and transparency than provided by qualitative or conceptual approaches or by expert opinion only. The benefits of a quantitative model are greatest where local ecosystem and

evolutionary dynamics are known, and when primary sources of uncertainty are considered.

ADVANCEMENTS THROUGH RESEARCH

Despite the rapid pace of research on coral biology and conservation that is occurring on a global scale, there are many gaps and unresolved issues that need to be addressed in the short and long term. Priority research would improve understanding of the risks and benefits associated with a potential intervention and reduce critical uncertainty to better inform decision making and modeling. These priorities include improved ways to identify, measure, and monitor fitness parameters of corals; greater understanding of factors that contribute to stress tolerance and associated tradeoffs for corals; and measuring the impact of interventions on demographic processes within reef ecosystems.

Research on Fundamental Coral Reef Biology

Effective intervention approaches for reefs require an improved understanding of which factors underpin coral health and how these lead to reef resilience at scale. Though these topics are inherently broad, there are a number of research areas that can be prioritized. These areas include the following:

- Identifying the cellular mechanisms of bleaching, and how these pathways are influenced by recent thermal history, host genetics, symbiont type, and microbiome.
- Identifying underlying causes of coral diseases, and developing biomarkers of coral health, heat susceptibility, and disease diagnosis as well as ecosystem health.
- Determining functional roles of, and tradeoffs among, members of coral reef communities at multiple ecological scales from coral-associated symbionts and microbiomes up to the composition of coral species in reef communities.
- Identifying population structure, determining evidence for local adaptation, and defining relevant management units for population recovery.
- Developing methods to improve recruitment and survivorship of corals that are released, planted, relocated, or settled on reefs at the reef scale.
- Developing extensive, freely available databases on coral hosts, symbionts, and microbiomes to support studies on population structure, genotype-phenotype relationships, population structure, and community dynamics.
- Identifying species-specific threshold responses of corals to changes in temperature, light incidence, and ocean pH, as well as reef-scale threshold responses to disturbance and environmental change.

Site-Specific Research and Assessment

Development of appropriate ecological models and identification of relevant management objectives and goals requires site-specific information. The committee highlighted the assessments that would inform robust decision-making processes. These items include the following:

- Identifying local stressors that influence population recovery and determining whether stressors are likely to influence the success of interventions.
- Developing appropriate metrics and recovery goals that assess the effects of the intervention on ongoing tolerance, health, fitness, and recruitment within the target management unit as well as on connected reefs.
- Evaluating whether population recovery at a specific site can be achieved through translocation or managed breeding and if so, which intervention is most appropriate.
- Identifying host, symbiont, and microbial populations at restoration sites, to ensure treatments or manipulations aimed at improving coral physiological performance can achieve recovery goals.
- Assessing in a site-specific manner the benefits, risks, and chances of success for implementing environmental interventions.
- Identifying the most appropriate site-specific, synergistic management and intervention strategies that together provide greater chance of success and reduced risks than the sum of the impacts of each intervention alone.

Research to Improve Specific Interventions

Research is needed to stage interventions from laboratory experiments to full-scale management strategies. Additionally, research can help inform the safety, efficacy, and cost-efficiency of interventions. Priority research to support these goals include the following:

- Developing protocols for control of pathogens (biosecurity and quarantine).
- Developing effective approaches to modify symbiotic algal and/or microbiome populations.
- Developing effective approaches to determine whether corals that are released, planted, relocated, or settled on reefs contribute to recovery goals, while reducing risk to ongoing adaptation and ecological processes.
- Developing and testing genome-editing methods in a wide variety of ecologically important coral species.
- Developing methods of delivery for nutrients, probiotics, antibiotics, phage therapy, and antioxidants at reef scales.
- Assessing feasibility, potential benefits, costs, limitations, and risks associated with environmental interventions.

Research to Inform Risk Assessments and Modeling

The adaptive management cycle requires monitoring and evaluating the results of a management action based on an established monitoring program in order to iteratively gain knowledge and improve information to support decision making. Thus, ongoing improvements to structured decision making requires:

- Targeted monitoring to evaluate performance, improve benefits, and minimize or manage risks.
- Iterative model design to reduce uncertainties and improve model predictions to increase confidence in the decision support framework.

THE TROPICAL WESTERN ATLANTIC AND CARIBBEAN CASE STUDY

The committee was tasked with assessing coral intervention strategies and their ability to meet objectives for sustaining coral reefs in the Caribbean and tropical western Atlantic. Coral reefs in this region show widely variable conditions, but many areas have experienced uniquely devastating losses in recent history. These losses have been due to a wide variety of factors including widespread local stressors, disease outbreaks, hurricanes, and bleaching events.

Ecological decline of Caribbean reefs appeared to accelerate in the late 1970s. Basin-wide major disease epizootics have been responsible for some of the greatest changes, with the loss of both the structurally dominant elkhorn and staghorn corals (*Acropora palmata* and *A. cervicornis*), followed by the loss of a keystone herbivore, the black-spined sea urchin (*Diadema antillarum*). Overfishing has compounded the impacts of the loss of *Diadema*, and the invasive lionfish, which has also spread rapidly through the region, has aggravated the impacts of overfishing by preying on juvenile fish. Poor land-use practices have also contributed to coral mortality by increasing sedimentation, nutrients, and turbidity. Recently, a virulent new disease, Stony Coral Tissue Loss Disease (SCTLD), has emerged in Florida and parts of the central and northeastern Caribbean, threatening coral diversity.

In addition to the significant impact of local stressors in the Caribbean, climate change impacts are increasing, and as elsewhere, there are limits to the effectiveness of local management in this context. Coral bleaching events have been observed widely across the Caribbean. Warming also affect corals indirectly by increasing intensities of tropical storms, and by triggering more devastating episodes of coral disease.

Implications for Selecting and Modeling Interventions

Assessing the conditions of Caribbean and tropical western Atlantic reefs helps clarify the attributes most relevant to selecting interventions, and influences analyses aimed at deciding which interventions to test and deploy. These attributes include generally poor reef conditions, intrinsic vulnerability, high interconnectedness, low diversity of coral and algal symbionts, high environmental variability across the region, and persistent and destructive disease outbreaks. The social attributes include a relatively widespread and growing network of coral restoration practitioners, located in a small (compared to the Indo-West Pacific) but politically complex region.

The committee identifies a range of opportunities for including interventions across management strategies and activities in the region. The following strategies seem the most promising for the tropical western Atlantic/Caribbean region based on the regional context dependencies and technical readiness across interventions. They represent options for more detailed evaluation using a model-based decision framework, including consideration of local management objectives and acceptable courses of action based on stakeholder input. They include:

- Identifying heat tolerant or disease resistant coral genotypes (and evaluating potential tradeoffs between these traits) among the Caribbean standing stock to provide opportunities for assisted gene flow, managed breeding, and genetic interventions.

- Leveraging existing coral restoration activities and infrastructure (involving the nursery propagation and outplanting of asexually-derived clones) to establish a comprehensive region-wide program to boost larval recruitment and survivorship.
- Exploiting sexual restoration activities to test algal symbiont manipulations.
- Expanding coral cryopreservation across the region to provide opportunities for managed breeding and assisted gene flow.
- Testing short-distance managed relocation (i.e., assisted gene flow) of corals across local thermal gradients, where disease incidence is not a limiting factor.
- Leveraging restoration activities to test pre-exposure methods to increase stress tolerance of outplanted corals.
- Assessing feasibility of environmental interventions to reduce heat stress at both local and sub-regional scales.
- Testing interventions, such as antibiotics, phage therapy, and microbiome manipulations, to halt the spread of emerging diseases, improve coral condition, and increase the success and/or feasibility of other interventions.
- Combining interventions where possible to increase resource efficiencies.
- Testing the efficacy of interventions under a range of different conditions by exploiting variability in the degree of degradation across the region.
- Developing regional and multinational coordination and agreements to meet the scale of the challenge.
- Soliciting and incorporating stakeholder input on interventions to gauge and maximize acceptability/social license.

Conclusion: Coral reef managers in the tropical western Atlantic/Caribbean region have a variety of interventions available to them depending on the localized management context and the specific objectives of stakeholders and decision makers. Available actions include leveraging existing restoration and propagation infrastructure, increasing sexual reproduction and genetic diversity of corals (managed breeding, gamete and larval capture and seeding, coral cryopreservation), capitalizing on thermally tolerant species and genotypes (managed selection, algal symbiont manipulation), accelerating reef connectivity to boost thermal tolerance when disease is not a factor (managed relocation), reducing disease spread (antibiotics, phage therapy, microbiome manipulation), and/or reducing exposure to stress (environmental interventions). The complex disease geography in the Caribbean requires particular care to ensure that interventions do not facilitate the spread or severity of ongoing disease outbreaks. These rapidly developing new interventions do not replace the need for direct management of local stressors.

Recommendation: The ongoing management and restoration efforts in the Caribbean provide a strong foundation on which to implement newly emerging interventions designed to increase the resilience of individual corals and coral populations. The modeling and decision-making tools outlined in this report should be used to inform more detailed assessments to evaluate which approaches might be appropriate for specific settings, including their interactions with more traditional management approaches. Maintaining genetic diversity in the face of multiple climate-driven stresses (e.g., bleaching and disease) is particularly important. Monitoring corals to maintain genetic diversity and identify resistant phenotypes should be simplified and standardized for research, ex situ

propagation, and in situ restoration. Research programs to model and field test the risks, benefits, and efficacy of interventions in this multinational and highly inter-connected region should be coordinated to maximize resources, co-learning opportunities, and the ability to achieve management objectives regionally.

1
Introduction

Coral reef managers are faced with a new decision crisis: deteriorating environmental conditions are reducing the health and functioning of coral reef ecosystems worldwide, creating a need for new management responses. Established tools for managing coral reefs are not sufficient, nor designed, to preserve coral reefs as the climate changes. Increasing episodes of sustained above-average water temperatures have increased the frequency of coral bleaching events—where corals expel their symbiotic algae—from which many corals do not recover (Hughes et al., 2018; NOAA, 2018). Increased temperatures are also linked to increasing disease prevalence, which has devastated reefs already in decline from multiple stressors (Carpenter et al., 2008; Harvell et al., 2007). As excess atmospheric carbon dioxide dissolves into the ocean and lowers the pH of seawater, corals will have a reduced ability to calcify and grow their hard skeletons that support the reef structure. These stresses will compound the impacts from local sources such as pollution, habitat destruction, overfishing, and invasive species (Bellwood et al., 2004; Pandolfi et al., 2003).

Local stressors have historically been the main cause of coral reef loss and degradation, and control of local stressors is integral to continued coral persistence (McLeod et al., 2019; but see Bruno et al., 2019 for questions regarding the contribution of local management to coral reef resilience). However, even in areas free from local stress, coral reef cover is being lost (Hughes et al., 2017a). At the same time, limiting future greenhouse gas emissions is necessary to maintain a global environment within which corals can survive; average temperature increases as little as 1˚C -2˚C can lead to coral bleaching (Donner et al., 2005; Frieler et al., 2013; Hoegh-Guldberg, 1999; Sheppard, 2003; van Hooidonk et al., 2013, 2014). These powerful changes have driven interest in approaches that improve the ability of corals to survive in a high emission environment (as described in NASEM, 2019). These “coral interventions” include those that affect the corals’ genetics, reproduction, physiology, ecology, or local environment. Many arise from a growing understanding of how the coral holobiont—the coral and its symbiotic algae and the rest of the microbiome—responds, acclimatizes, and adapts to stress. These interventions will alter the reef in some way, frequently by shifting population structures, altering genes, or changing the composition of symbiont communities. Their ultimate goal is stabilization or increases in coral cover, diversity, and reef functioning. However, these changes provide very different benefits across sites and may have unintended consequences that will similarly vary across locations.

A committee was convened by the National Academies of Sciences, Engineering, and Medicine to consider interventions that have the potential to increase the survival and persistence of coral reefs in deteriorating environmental conditions. This study was requested and funded by the National Oceanic and Atmospheric Administration, with additional support from the Paul G. Allen Family Foundation. In their first report (NASEM, 2019), the Committee described 23 interventions that have the potential to increase the persistence of coral reefs as environmental conditions deteriorate. While management of the entire reef community is essential for coral persistence and delivery of vital reef services, the interventions explored by the committee are

those that improve the resilience of individuals, populations, or communities of corals directly. Reef-associated species are often targets of existing management practices, such as control of overfishing and invasive species.

The committee has used the term "resilience" to refer to a system's ability to both resist disturbances and recover from them (Edmunds et al., 2019; Holling, 1973; Hughes et al., 2010). To date, most of the conventional approaches used to manage reefs, such as improving water quality and managing herbivores, have tended to focus on ways that facilitate the recovery potential of reefs following disturbances, and many of these approaches have drawn their inspiration from the study of Caribbean reefs (e.g., Hughes, 1994). Most of the novel approaches and interventions discussed in this report and its predecessor (NASEM, 2019) emphasize approaches that increase the resistance of the coral organisms to disturbances (particularly climate change and disease) in order to avert widespread coral mortality, or for the community to recover to a coral-dominated state on its own through inclusion of stress-resistant types. It should be noted that the committee included some interventions which may improve coral persistence by reducing their exposure to disturbance, though may not improve their resilience.

These interventions are summarized in Table 1.1. The interventions fall into the four categories:

- **Genetic and reproductive interventions** provide an opportunity for increased selection and breeding of stress-tolerant traits that may improve the resilience of coral populations and species. In addition to naturally resilient corals or members of their microbiome, genetic manipulation may provide the opportunity to create corals that can withstand increasingly severe environmental conditions.
- **Physiological interventions** influence the physiological responses of corals without changing their genomes (though it may be through genetic mechanisms) through improvements in health and resilience.
- **Coral population and community interventions** seek to directly alter the composition of an entire population or communities of corals through managed relocation at varying scales—from movement within their range to across ocean basins.
- **Environmental interventions** reduce exposure of coral reefs to increasing temperatures or acidifying waters at a local level (as opposed to methods of global climate engineering).

The previous report reviews the state of science on each of the interventions covering the following categories: What it Is, How to Do It, Benefit and Goals, Current Feasibility, Potential Scale, Risk, Limitations, and Infrastructure. The report is a snapshot of a fast-moving field of research; for example, since publication of the report, Hagedorn et al. (2018) published their demonstration of the use of cryopreserved coral sperm to conduct assisted gene flow across genetically-isolated *Acropora palmata* populations in the Caribbean. While the information in the first report informs the framework laid out in this second report, it is important to realize that the state of science will continue to change. New ideas might arise, uncertainty might diminish, and perceptions of risks and benefits may change with new information.

TABLE 1.1 Overview of Interventions Examined in the Committee's First Report

Intervention	What It Is	Current Feasibility	Potential Scale	Limitations	Risks
Genetic and Reproductive Interventions					
Managed Selection	Creating increased frequency of existing tolerance genes	In laboratory and at small local scales	Local reef scale; potentially transgenerational	Needs large populations	Decrease in genetic variation
Managed Breeding: Supportive Breeding	Enhancing population size by captive rearing and release	Success with some species at small scales	Local reef population; potentially transgenerational	Depends on sufficient population sampling and recruitment success of released individuals	Decrease in genetic variation
Managed Breeding: Outcrossing between Populations	Introducing diversity from other populations through breeding	Demonstrated in laboratory for a few species	Local reef population; potentially transgenerational	Requires transport of gametes or colonies across distances and field testing across generations	Outbreeding depression; native genotypes may be swamped
Managed Breeding: Hybridization between Species	Creation of novel genotypes through breeding	Demonstrated in laboratory for a few species	Local reef population; potentially transgenerational	Limited ability to create hybrids; requires testing for fertility and fitness	Outbreeding depression; competition with native species
Gamete and Larval Capture and Seeding	Collection and manipulation in the field and laboratory and release into the wild	Feasible at local scales	Laboratory to local reef scale; potentially transgenerational	Site-specific reproductive timing, recruitment success can be poor	Limited genetic diversity; selection for laboratory versus field success
Coral Cryopreservation	Frozen storage of gametes and other cells for later use and transport	Feasibility is high for sperm, and growing for other tissue types	Materials can be transported globally	Requires excess gametes, larvae, or tissues	Long-term survival uncertain; genetic variation reflects only current conditions
Genetic Manipulation: Coral	Altering coral genes for new function	Technically feasible for larvae	Would occur in laboratory; can be self-perpetuating	Gene targets and cellular raw material unidentified, long lead time to roll out to reefs	Might alter wrong genes; unknown risks
Genetic Manipulation: Symbionts	Altering symbiont genes for new function	Not yet feasible	Would occur in laboratory; can be self-perpetuating	Technology not established; gene targets and cellular raw material unidentified	Might alter wrong genes; kill target cells; unknown risks
Physiological Interventions					
Pre-exposure	Using stress exposure to make colonies more tolerant	In laboratory and small-scale field trials	Local reef scale; may be temporary or transgenerational	Difficult to scale up beyond local	Could be detrimental if applied incorrectly

Algal Symbiont Manipulation	Changing algal symbionts to more tolerant types	Observed after bleaching events; demonstrated in laboratory	Individual coral colony or large spawning events; unknown longevity	Difficult to scale; easier for some coral species than others	Ecological tradeoffs, e.g., slower growth
Microbiome Manipulation	Maintaining/increasing abundance of the native or new beneficial microbes	Demonstrated in laboratory and nursery facilities for limited coral species	Locations on reefs to reef scale; applied at times of stress	Reef-wide delivery mechanisms are lacking; lack of known beneficial microbes; little understanding of direct or indirect effects	Potential to increase deleterious microbes, decrease beneficial ones
Antibiotics	Adding antibiotics to control pathogenic microbes	Used in aquaculture and demonstration in small-scale field trials	Laboratory, aquarium, and colonies on reef; requires repeated application	Lack of specificity to target pathogens limits effectiveness	Promote antibiotic resistance in deleterious microbes; destabilization of native beneficial microbiomes
Phage Therapy	Adding phage viruses to control pathogenic microbes	Demonstrated in laboratory experiments	Local reef scale; potential to self-propagate	Lack of identified target coral pathogens	Undesirable gene transfers across microbial populations; impact on beneficial microbes
Antioxidants	Reducing cellular oxidative damage derived from stress using chemical treatments	Demonstrated in some laboratory experiments	Laboratory only; requires repeated application	Little understanding of direct or indirect effects	May affect other reef species
Nutritional Supplementation	Using nutrients to improve fitness and increase stress tolerance	Regular use in coral research and aquaculture	Laboratory and aquarium; requires repeated application	Poor understanding of balanced coral diets; reef-wide delivery mechanisms are lacking	Shifts carbon, nitrogen, and phosphate balance and may benefit coral competitors
Coral Population and Community Interventions					
Managed Relocation: Assisted Gene Flow	Increasing abundance of stress-tolerant genes or colonies within population range	Technically feasible with information gaps regarding successful methods	Regional reef scale; can be permanent	Uncertain maintenance of stress tolerance over time	Moving nontarget genes; ecological tradeoffs
Managed Relocation: Assisted Migration	Moving stress-tolerant or diverse genes or colonies just outside species' range	Technically feasible with information gaps regarding project design	Regional reef scale; can be permanent	Uncertain maintenance of stress tolerance and persistence over time between locations	Moving nontarget genes, species, and microbes; ecological tradeoffs

Managed Relocation: Introduction to New Areas	Moving stress-tolerant or diverse genes or colonies to new regions	Untested though technically feasible with information gaps regarding project design	Global movement impacting individual reef scale; can be permanent	Uncertain maintenance of stress tolerance and persistence over time between locations	High risk of moving nontarget genes, species, and microbes; ecological tradeoffs
Environmental Interventions					
Shading: Atmospheric	Sky brightening to relieve light and heat stress	Untested	Local to regional scale; temporary	Needs appropriate atmospheric conditions and technology	Altered light regimes; aerosol (salt) deposition
Shading: Marine	Reducing sunlight to relieve light and heat stress	Operational at small scales	Sites within reefs; temporary	Retention and advection limit application	Altered light regimes; plastic pollution
Mixing of Cool Water	Pumping cool water onto reef to reduce heat stress	Small-scale field tests with unknown efficacy	Local reef scale; temporary	Energetically costly or impossible to scale up	Altered physical and chemical (pH, nutrients) regimes
Abiotic Ocean Acidification Interventions	Reducing CO_2 levels chemically	Effective in small-scale laboratory experiments	Sites within reefs depending on environmental setting; requires consistent input	Costly to scale up chemical quantities	Impact of chemicals on environment
Seagrass Meadows and Macroalgal Beds	Reducing daytime CO_2 levels biologically	Some efficacy shown in field measurements	Local reefs depending on environmental setting; long-term benefit	Limited environmental settings; need to remove macroalgae	Detritus; altered nutrient loads; competition from macroalgae; increased CO_2 at night

STUDY TASK AND APPROACH

Coral interventions have varying degrees of benefits and risks, and there are varying degrees of probability and certainty around these benefits and risks. At the same time, there is a strong possibility that the risks of not intervening to increase coral persistence are growing as greenhouse gases continue to accumulate. Moreover, different interventions vary in their feasibility in different places and at different times. Whether action or inaction on specific interventions is more likely to produce coral reef gains is the heart of the decision that will need to be made in local regions across the tropical oceans.

In this report, the committee builds upon its first report by outlining the necessary components of a structured decision process and providing an example framework within which to evaluate the information available about risks and benefits of novel interventions. The specific tasks of the committee are outlined in Box 1.1; this report addresses items 2 through 5. In addition to the workshops held in Miami, Florida and Honolulu, Hawaii during the development of their first report, the committee held an open meeting on October 30, 2018 in Washington, DC with experts in decision science to explore these elements of their task.

BOX 1.1
Statement of Task

An ad hoc study committee will be assembled to review the science and assess potential risks and benefits of ecological and genetic interventions that have potential to enhance the recovery and persistence of coral reefs threatened by rapidly deteriorating environmental conditions that are warmer, less favorable for calcification, have impaired water quality, and pose continuing disease threats. Given these environmental conditions, the committee will consider interventions to address near-future (e.g., 5-20 years) and long-term environmental scenarios as part of an overall risk assessment in an ecosystem context. The coral intervention strategies will be assessed with regard to the goal of increasing the long-term persistence and resilience of tropical coral reefs and their ecological functions. Specifically, this review shall:

1. Review and summarize scientific research on a range of intervention strategies, either designed specifically for coral or with the potential to be applied to coral, including evaluation of the state of readiness. Strategies of interest include, but are not limited to, stress-hardening, translocation of non-native coral stocks or species, manipulation of symbiotic partnerships within the coral holobiont, managed selection, genetic modification, and to the extent possible, proposed engineering solutions to promote reef persistence, such as shading/cooling during bleaching events.

2. Provide an environmental risk assessment framework for evaluating the likelihood of potential ecological benefits and harms of the novel interventions. The framework will include the following elements, as probabilistically as possible, to support decision making.

- Assess the likelihood that implementation of particular intervention strategies will substantively improve the persistence and resilience of coral reefs and their ecological functions, including support of reef-associated ecosystems and fisheries, over and above conventional management regimes;

- Describe the nature and likelihood of predicted risks (e.g. disease introduction; loss of reefs, ecological functions, or coral species) and potential unintended consequences (e.g., species invasions, loss of genetic diversity) and tradeoffs of specific intervention strategies;
- Assess the relative harms and benefits of different interventions compared with one another and the status quo of conventional management techniques.

3. Develop a decision pathway (a conceptual sequence of events) spanning initial research, laboratory and field-based research, to implementation and monitoring of the potential interventions. The pathway will include identification of specific ecological criteria or thresholds (e.g. population or environmental tipping points such as onset of annual bleaching) that may justify implementation of a more risky intervention strategy depending on the magnitude and urgency of the degradation. Case studies may be used to illustrate how the decision pathway could guide selection of an intervention strategy under different scenarios of near-future conditions for tropical coral reef systems.

4. Identify the research needs to refine the intervention strategies and reduce uncertainties in the environmental risk assessments. The research should include activities that could increase confidence in predicted net benefits and minimize, avoid, or mitigate risks of implementation.

5. Assess interventions under near- future conditions (e.g., 5-20 years, as projected under the IPCC Representative Concentration Pathway 8.5) for Atlantic/Caribbean coral reef systems based on the risk assessment framework and available information. Intervention strategies should be assessed relative to the objectives and performance measures, identified by the committee, for sustaining coral reefs and their ecological functions. Interventions should be characterized, using designations such as "not appropriate", "needs further investigation", "feasible for field testing", "feasible for implementation. Atlantic/Caribbean coral reef systems are specified for this assessment due to their advanced state of coral reef degradation, less complex ecological conditions (e.g., smaller basin, lower diversity), and imperiled status of foundational reef building coral species, compared to the Indo-Pacific.

Two reports will be produced. The first interim report will address task 1 and second report will address the other elements of the task.

This study is focused on the state-of-the-science of novel intervention strategies to identify and compare potential ecological risks and benefits. Although these interventions also raise societal, policy, legal, and likely ethical implications for decision making, these considerations are beyond the scope of this review. Effectiveness of reef management and restoration activities currently underway will be considered only to the extent that they set a baseline for use in the risk assessment of the novel interventions.

The committee is not tasked with developing a framework that can be immediately applied to an individual area. This is primarily because it is outside the committee's task to consider the social, policy, legal, and ethical drivers that would be central to any management decisions. Because these drivers need to be defined and comprehensively explored with a broad set of stakeholders for any specific decision, the committee's goal is to highlight universal concepts and best practices of structured decision making, and provide an illustrative model of a simplified reef

and decision scenario based on an example set of interventions. In Chapter 2, the committee first reviews the interventions from the first report to assess their practical readiness and context dependencies to illuminate how managers may select interventions most suited to their situation for further assessment in a decision framework. Chapter 3 describes the best practices for structured decision making and risk assessment for taking an intervention from research to inclusion in a management strategy, and the available decision tools that have been, or might be, applied to coral reef management. In Chapter 4, the committee provides an illustrative model and decision analysis to exemplify the challenges and insights associated with decision making around coral interventions. In Chapter 5, the committee identifies research areas that would inform decision making by improving understanding of the baseline reef system, assessing risks, and managing the beneficial impacts of potential interventions. Finally, Chapter 6 highlights the tropical western Atlantic/Caribbean region as a case study for how managers may consider their individual context and objectives in an evaluation of possible intervention strategies.

REEF MANAGEMENT CONTEXT

The process described in this report is meant to guide a particular component of the reef management decision process, where reef managers and other decision-makers evaluate the risks and benefits of using innovative interventions within their restoration and conservation programs. Overarching questions driving the selection and implementation of interventions presented in this report begin with addressing the present status and trends of coral reefs in a jurisdiction, the needs of stakeholders, and the mandates of local, state, and federal regulatory agencies. While the committee does not incorporate these broader questions into their example framework, highlight here are the intersections with the committee's task and other management considerations.

Management objectives against which to evaluate interventions are driven by the state of the ecological community and physical environment, local priorities, and risk tolerance in a particular area as well as ethical, economic, cultural, and legal constraints. A clear articulation of objectives is a vital component of the decision process described in this report. Management agencies have the dual responsibilities of protecting both reef resources and the people who depend on them. Thus, the anticipated outcomes of any intervention will be tied to the objectives of affected human communities. Because these ecosystems provide a variety of ecological, cultural, and economic services, and are at various stages of health, the selection of interventions will vary among sites and jurisdictions. For example, to address the need for coastal protection from wave damage, coral species with massive growth morphologies might be the appropriate choice for restoration and management objectives, as they are often more resistant to wave energy, sediment, and turbidity than branching corals (Ferrario et al., 2014). Alternatively, to replace essential fish habitat through enhanced rugosity, the use of branching, table, columnar, and arborescent growth forms would be appropriate (Komyakova et al., 2018). Rugosity, or structural complexity, is also an important attribute supporting coral larval recruitment, and provides spatial refugia for UV sensitive and less competitive species and life history stages. Such differences in objectives from place to place might be a common feature of coral management. The clarification of these objectives is an important starting point in the evaluation of management options, described further in Chapter 3.

A key influence on management options is the existing regulatory framework, where management authorities, such as permitting and other approvals, are distributed across local, regional, state, and/or federal entities. For example, in the United States, there are eight jurisdictions that possess and regulate reef-building corals: the states of Florida, Hawaii, and Texas; the Territories of American Samoa, Guam, and the U.S. Virgin Islands; and the Commonwealths of the Northern Mariana Islands and Puerto Rico. The U.S. federal government has sole authority and responsibility for other coral reef areas including the Pacific Remote Islands (U.S. Minor Outlying Islands) which are part of a Marine National Monument. Additionally, there are the three Freely Associated States, which receive federal funding under the Compacts of Free Association (the Federated States of Micronesia, the Republic of the Marshall Islands, and the Republic of Palau). In all cases, any activity that includes U. S. federal funding must comply with the appropriate U.S. federal regulations.

There are 14 laws and statutes that regulate activities involving corals in the United States (summarized in Richmond et al., 2007):

- 1899 – Rivers and Harbors Act (33 U.S.C. § 403)
- 1900 – The Lacey Act (16 U.S.C. §§ 3371–3378)
- 1958 – Fish and Wildlife Coordination Act (16 U.S.C. §§ 661-667e)
- 1969 – The National Environmental Policy Act (NEPA) (codified as amended at 42 U.S.C. § 4321 et seq.).
- 1970 – Council for Environmental Quality (sec. 201 [42 U.S.C. §§ 4341–4347 and 4372–4375] under NEPA)
- 1972 – Coastal Zone Management Act (codified as amended at 16 U.S.C. §§ 1451-66)
- 1973 – Endangered Species Act (16 USC §§ 1531-1544)
- 1975 –Convention on International Trade of Endangered Species of Wild Fauna and Flora (CITES; the United States is a signatory)
- 1977 – Clean Water Act (codified as amended at 33 U.S.C. §§ 1251-1387)
- 1980 – The Comprehensive Environmental Response, Compensation, and Liability Act (CERCLA) (codified as amended at 42 U.S.C. §§ 9601-9675)
- 1996 – Magnuson-Stevens Fishery Conservation and Management Act (codified as amended at 16 U.S.C. §§ 1801 et seq.).
- 1998 – Executive Order No. 13,089, 3 C.F.R. § 193 on Coral Reef Protection
- 2000 – Executive Order No. 13,158, 3 C.F.R. § 34909 on Marine Protected Areas
- 2000 – Coral Reef Conservation Act (16 U.S.C. §§ 6401 et seq.)

The overriding philosophy behind a set of regulations is to prevent activities that harm corals and coral reefs. This can create challenges for activities and interventions that intend to restore reef resources but that also have unintended or unknown risks. By permitting and/or funding these activities, the various federal and local agencies balance allowing activities that might damage corals with the likelihood of damage should no action be taken. Without a clear recognition of how and when inaction could result in greater resource losses than the interventions identified by the committee, there may be difficulty fitting new interventions into the existing regulatory framework. It is important that addressing the regulatory and policy framework for intervention implementation be undertaken concurrently with the scientific and management directed tasks. While this is not within the scope of this report, the ability to evaluate risks and benefits, which

is the focus of the report, will still be important for informing future regulatory and policy changes.

Social Capital and Stakeholder Buy-in

Coral reefs are social-ecological systems; humans are responsible for the greatest threats to reef persistence and resilience, yet are also among the primary beneficiaries of healthy and functional coral ecosystems that provide a variety of ecosystem services and benefit streams (Anthony et al., 2015; Aswani et al., 2015; Cinner et al., 2009; Folke, 2006; Hicks et al., 2015; Kittinger et al., 2012). Under global environmental change, ecological, economic, and social elements of reefs will all be affected, and both conventional and new management strategies thus need to incorporate the environmental and human dimension. With the well-recognized economic, ecological, and cultural benefits of coral reefs to hundreds of millions of people worldwide (Burke et al., 2011), there are many stakeholder groups that are interested and involved in the decisions surrounding interventions that sustain these ecosystems. There is an important role for the social sciences to be included in future intervention study design, implementation efforts, and the collection of evaluation effectiveness metrics.

Management Resources

A decision pathway from theory to practice involves a multitude of stakeholders. Novel approaches have originated from the growing understanding of coral biology and ecology, which inspires new theories upon which new interventions are built. While experimentation in controlled laboratory settings can inform the potential of many intervention approaches, moving into the field improves real-world understanding. This will significantly increase capacity needs, including for data collection and development of models that support decision making. Additionally, cooperation and collaboration with resource managers in one or multiple jurisdictions will inform research priorities and ensure regulatory compliance. Coordinating and convening activities amongst managers and stakeholders help integrate management strategies, align science with policy, and facilitate buy-in from the general public. In the United States, the Coral Reef Task Force established in 1998 under Executive Order 13089 is already functioning in this convening role and can move quickly to develop guidance and lines of responsibility for intervention strategies.

When developing their first report, the committee was unable to find or estimate potential costs of deploying the interventions; however, just like risks and benefits, costs are likely to vary across interventions and over time. Generally, research and development costs will be high in early stages, and can decrease as technologies are refined. For example, initial costs of selective breeding might include genotyping, husbandry, outplanting of offspring, and monitoring. Some of these costs might be able to be estimated but only in a research setting, and not at regional or global scales. Deployment after the research and development phase can require large investments in infrastructure or in operations, depending on the intervention. It is important to note that costs of deploying an intervention would be evaluated against the expected benefit, as well as the cost of inaction. It is not in the committee's scope to do a cost-benefit analysis, but it is important to note that the ecosystem services provided by coral reefs provide high monetary value (e.g., Beck et al., 2018; Costanza et al., 2014; Storlazzi et al., 2019) and expensive

approaches could be justified. For example, the Great Barrier Reef contributed an estimated $6.4 billion to the Australian economy from 2015-2016, mainly from tourism but also from fishing, recreation, and scientific activities (Deloitte Access Economics, 2017). Global estimates of the economic value of coral reefs to fisheries, tourism, coastal protection, and biodiversity value (research, conservation, and nonuse) are on the order of $30 billion (Burke et al., 2011; Cesar et al., 2003).

The scale of the problem is massive; global environmental change is causing tropical reefs around the world to be susceptible to increasing loss and degradation. Reef managers will necessarily be addressing coral reef persistence at smaller scales. An important, though not essential, consideration for selecting interventions is their ability to be implemented at relatively large scales. Many small-scale efforts are possible, but expensive. Interventions that depend on coral gardening approaches will benefit by improvements made in the field of restoration. Scalability can be achieved through research, such as in the development of new treatment methods. For example, it is possible to treat individual coral polyps or colonies with antibiotics or nutritional supplements, but there are no known methods of deployment to an entire reef without expensive individual treatments or risky broadcasts to an entire reef. Ultimately, the ability to scale the wide-ranging approaches will vary.

2
Selecting Interventions for Decision Analysis

The committee identified 23 types of coral interventions in their first report (Table 1.1), and even within these 23 options, there are further options and choices that can be made. As a consequence, coral reef managers are faced with the task of evaluating the benefits and risks of a growing number of interventions, separately and in combination. Several questions will help narrow the array of options. Foremost is whether the state of research has progressed sufficiently that they are ready to be deployed. However, there is still value in assessing the potential risks, benefits, and utility of interventions that are not immediately "ready," to evaluate the value in pursuing a research program to improve their practical readiness. Additionally, a manager will want to consider which interventions are appropriate for a particular reef, community, and environment. Within a region, there may be specific areas better for testing interventions, distinct from areas where the interventions are likely to have a greater benefit or chance of success. Lastly, the relationships between interventions—such as shared biological or infrastructure resources—may increase stakeholder interest in investing in a set of interventions. The overarching goal of this chapter is to provide answers to the questions: "What can a manager decide to do now and what can they expect to have available in the near future? What interventions are suited for the local ecological and management context?" The answers will help define the set of opportunities for consideration in a decision analysis used by local agencies and communities.

TIMEFRAME TO TECHNICAL READINESS

The coral interventions detailed in the committee's first report (NASEM, 2019) represent a wide range of strategies that have very different levels of practical development. In this section, the committee first identifies interventions that managers could decide to evaluate for implementation now. The next identified interventions that seem likely to be available at a local scale in approximately 2-5 years. Last are interventions that may need longer-term (5-20 year) investments, either because the technology to do them is not yet available or because coral growth for multiple generations is required. This assessment is largely based on the state of research described by the committee in their first report. It is important to emphasize that while an intervention may be technically ready to deploy, its acceptability for meeting management goals and other social values is essential to address, and its anticipated risks and benefits assessed before deployment (discussed further in Chapters 3 and 4). Additionally, its current effectiveness may be more limited in time or space than is required to meet a management objective. Further research may be valuable even for this class of interventions to lessen risks or improve benefits (discussed further in Chapter 5). Research on developing the practicality of interventions that are nearly ready may help provide these tools in a time frame that is useful for decision makers. Long-term investments in both laboratory-based research and field testing may be needed to make the last set of interventions practical and widely available.

The committee has organized a three-tiered approach to resilience intervention: Immediate, short-term development, and long-term development interventions. Interventions in the "Immediate" (I) category might help stabilize and improve local reefs in the face of current climate but may not be enough as climate continues to worsen. The interventions in the "Short-term" (S) development category, once available, could strengthen resilience even further. Likewise, deployment of the short-term development interventions may help stabilize and improve reef populations while the "Long-term" (L) development interventions are developed and come on-line (Figure 2.1). Interventions across categories thus build on one another, and effectively may also buy time until greenhouse gas emissions can be reduced or removed.

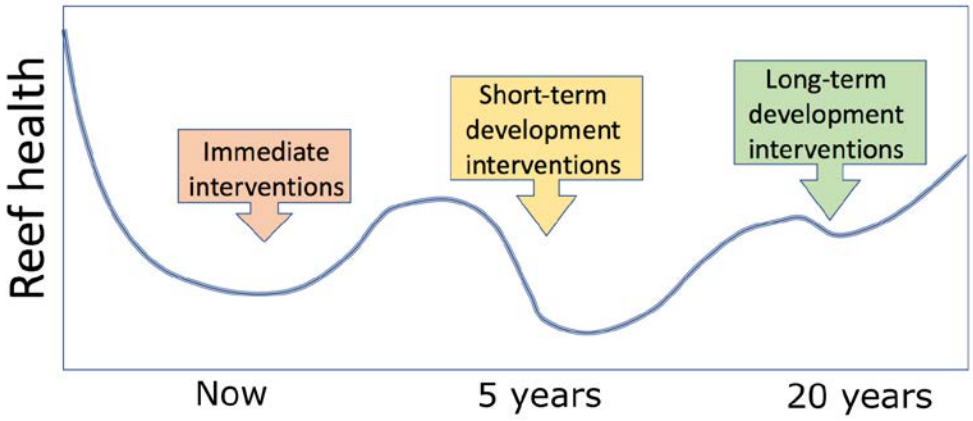


Figure 2.1 A conceptual depiction of staged implementation of interventions. Theoretically, immediately available interventions may provide enough increase in coral resilience so they persist until short- and long-term development brings a broader array of interventions, capable of supporting corals in continuously worsening conditions, into a state of readiness.

Interventions Available Immediately (I)

Supportive breeding (I) can be done with many corals by collecting gametes during annual spawning (a broadcast release of gametes), followed by fertilization, larval rearing, and outplanting at the location of collection. For some species, larvae can be collected directly from colonies on a regular basis. Constraints include limited windows for larval release or spawning, low survival of larval settlers, and the labor involved in large-scale husbandry efforts. Population size enhancement can be achieved with fragmentation and growth of colonies in nursery settings. These restoration efforts are currently the most often used on reefs. When colonies are chosen for breeding or fragmentation based on particular traits, such as heat resistance, then this is also considered **managed selection (I).** Testing corals for heat resistance and using them in nurseries is available as a strategy now (Morikawa and Palumbi, 2019). Scaling up these approaches requires increases in costs, labor, reef space, and donor colonies.

Assisted gene flow (I) is similarly available and differs from the above in that larvae or fragments available for outplanting are chosen for their high resistance to heat (or other traits) and then moved into new locations within their range where these genes or colonies do not occur or are rarely present. Finding and mapping heat resistant colonies is currently possible, but

requires marine research or aquaculture facilities for testing. Small, inexpensive, and portable tools to assess stress tolerance would expand development of this approach.

Gamete and larval capture and seeding (I) can be accomplished during periodic larval release and annual spawning cycles in most ocean aquaculture or research facilities (Chamberland et al., 2015, 2016, 2017). Its impact is limited by the number of days a year in which larvae or gametes can be collected, and the number of larvae that can be reared. Most corals are spawners, releasing eggs and sperm into the water column over limited periods each year, ranging from a couple of nights during a single lunar cycle to several nights over multiple months. Brooding corals that release fully developed larvae may do so nearly daily, monthly, throughout the year, or only during several months. As such, the use of gamete and larval collections is both location and species dependent. The products of this approach are used in **supportive breeding** or **assisted gene flow**, described above.

Pre-exposure (I) to heated conditions has been demonstrated to increase heat resistance in numerous acclimation experiments in laboratory settings and appears practical for short periods at least. Pre-exposure to particular temperature or irradiance regimes has long been recognized as being an important determinant of stress tolerance in the field (e.g., B. Brown et al., 2002; McClanahan et al., 2005) and temperature regimes which pre-expose corals to a mild warming episode prior to severe heating have been shown to offer some protective value against bleaching on the Great Barrier Reef (Ainsworth et al., 2016). Depending on the mechanism by which increased resilience is achieved, the effects of pre-exposure may be temporary, declining in days or weeks if due to reversible changes (e.g., temporary changes in gene or protein expression), but may be more long-lived (e.g., B. Brown et al., 2015) if due to epigenetic, maternal, or microbiome effects (Putnam and Gates, 2015). Wide-scale sub-lethal reef heating has not yet been developed as a bleaching mitigation intervention strategy, although pre-exposure of corals to bleaching stressors prior to outplanting is being trialed as part of restoration efforts (Cabral et al., 2018; Winter et al., 2018).

Likewise, **algal symbiont manipulation (I)** of adult corals has been shown to increase heat resistance if *Durusdinium* symbionts replace *Cladocopium* and other genera, both in the lab (Cunning et al., 2015, 2018; Silverstein et al., 2015) and the field (Berkelmans and van Oppen, 2006). However, such replacements, when they occur naturally on reefs following bleaching events, may be temporary, lasting only months to years (LaJeunesse et al., 2009), although some shifts may have occurred on reefs that are more long-lived (decades, Edmunds et al., 2019). Algal symbiont communities can also be manipulated at earlier life history stages by raising coral juveniles in different reef environments (e.g., Abrego et al., 2009). Most coral species produce gametes without symbionts, and the larvae or recruits can be introduced to specific symbionts in a laboratory or other controlled environment (e.g., Little et al., 2004, McIlroy and Coffroth, 2017; Williamson et al., 2018). However, the longevity of these directed changes may be relatively short-lived (weeks-months) if the environmental conditions in which the recruit is raised do not favor the new symbionts (Abrego et al. 2009; Coffroth et al., 2001).

Coral cryopreservation (I, S) is poised now to help accelerate **gamete and larval capture and seeding**, **selective breeding**, and **assisted gene flow** (Hagedorn et al., 2018). Freezing gametes for future use would greatly expand opportunities for rearing and reduce the risks of coral

transportation that limit use of **managed relocation** (see below). Sperm storage has been shown to be effective, and such gametes can fertilize eggs (Hagedorn et al., 2017). As a result, sperm storage is immediately available. While coral larvae have been successfully cryopreserved (Daly et al., 2018), egg storage and egg revival for fertilization has yet to be demonstrated.

Interventions Potentially Available in a Short-term (S) or Long-term (L) Timeframe

Managed breeding—outcrossing between populations (S) can be done by bringing gametes together from corals from different populations adapted to different habitats. Outcrossing requires genetic differentiation across multiple loci between pairs of parents, and generally this demands medium- or long-distance transport. As a result, this intervention has been traditionally limited by the distances over which corals can be moved during spawning. Programs in laboratory-based spawning have demonstrated success, meaning that corals can first be moved long distances for this work and then brought into spawning condition (Craggs et al., 2017). Alternatively, cryopreservation of gametes can also facilitate this intervention over any distance. Success in these efforts is delayed by the need for multi-year grow out of larvae to produce sexually reproductive adults and by the need for rapid mapping of coral genetic differentiation across multiple spatial scales for multiple species so that the degree of outcrossing, and the potential genetic effects can be controlled.

Managed breeding—hybridization between species (S) can be done by cross fertilizing different species. It does not require long distance movement of the parent corals if the species are sympatric. Success is limited by cross-fertilization ability of different species (and potentially the fertility of the hybrids), for which there has only been demonstration in relatively few species (Chan et al., 2018; Willis et al., 1997, 2006). Readiness is also limited by the need for multi-year grow out of hybrid larvae.

Supplements to corals (**microbiome manipulation** (probiotics)**, antibiotics, phage therapy, nutritional supplementation,** and **antioxidants**) **(S)** have demonstrated effectiveness in laboratory or nursery/aquarium settings and in some cases, small-scale field trials (e.g., Atad et al., 2012; Hudson, 2000; Marty-Rivera et al., 2018; Rosado et al., 2018). However, limited knowledge about functional relationships between these interventions and coral health limits the ability to deploy them in a targeted, effective way. Nutritional supplements are in regular use in nurseries but delivery methods onto reef scales that would specifically target the coral, but not other taxa, are not developed. Application of antibiotics and phage therapy is also feasible, but limited by knowledge about the specificity of the antibiotics or bacteriophages to pathogenic bacteria. Similarly, limited knowledge of the functional role of particular bacteria and other components of the microbiome make targeted application difficult. Application of antioxidants has been trialed but knowledge about its feasibility for mitigating reactive oxygen species production during bleaching is rudimentary.

Ocean acidification interventions show feasibility at small scales. **Abiotic ocean acidification interventions (S)** (the addition of a strong base to elevate pH, or stripping carbon dioxide from the water column) have a demonstrated ability to increase pH (e.g., Albright et al., 2016; Koweek et al., 2016; Rau et al., 2007; Riebesell et al., 2010). However, the approaches are logistically limited by the difficulty of deployment on a reef at scales large enough to impact pH

and aragonite saturation. **Seagrass meadows or macroalgal beds (S)** located near coral reefs have been shown to raise local pH and the aragonite saturation state naturally (Manzello et al., 2012) and in flume experiments (Anthony et al., 2013). However, the benefit achieved from use of seagrasses and macroalgae will be limited by identifying the right water depth, water residence time, seagrass or macroalgae density, coral species, fate of fixed carbon, and other geographical, oceanographic, ecological, geomorphological, and meteorological attributes.

Cool water mixing (S), is conceptually simple but requires infrastructure difficult to install at even small reef scales. Reef cooling also faces the difficulty that cooled water is moved away from reefs and diluted by local currents.

Shading interventions, similar to cool water mixing, address resilience indirectly, not by increasing heat resistance but by reducing temperature and light stress that is associated with bleaching (although they could be used as a reef scale technique during regional thermal stress to maintain sub-lethal stress levels that contributes to hardening). **Marine shading (S)** technologies have been proposed to reduce light by creating physical or chemical barriers at the water surface or in the local atmosphere. Water surface barriers are easy to imagine, but the simplest ones like plastic sheeting could have disastrous consequences due to entanglement and pollution. Thin chemical barriers that are biodegradable and safe, yet also significantly reduce light, require research, development, and testing. **Atmospheric shading (L)**, by using salt aerosols to brighten and increase cloud cover, for example, has been theorized based on natural phenomena and empirical evidence but not tested (Alterskjær et al., 2011; Latham et al., 2013; Zhang et al., 2018). These interventions have also not yet been thoroughly evaluated for unintended consequences.

Genetic manipulation of corals and algae (L) has attracted a great deal of attention but is likely to be a practical intervention only over longer timeframes. Genetic manipulation of coral larvae has been achieved through use of CRISPR/Cas9 genetic constructs (Cleves et al., 2018), but adding exogenous DNA to symbiont cells has so far been unsuccessful. Nevertheless, rapid technology developments in DNA manipulation occurring across taxa may bring new tools to bear on these problems in the next few years, and dedicated research is likely to progress quickly. Likewise, targets for gene manipulation have not been identified. Assessing success of gene manipulation of corals would be required over multi-generation time scales through a series of growth periods (from manipulated larvae to sexual adults) each likely to be between 2-5 years. Genetic manipulation of single-celled symbionts would not require these long multi-generation steps. The combination of technology development, target identification, and grow out periods adds up to a decade or more time lag before being ready.

Managed relocation—assisted migration (L) and **introduction to new areas (L)** would be implemented in a similar way as **assisted gene flow.** However, increased distances of movement increase costs and decrease effectiveness in ways that are not yet well described (e.g., lower survival of coral individuals transported over great distances). As distances increase, risks from disease or invasive species introductions are probably also likely to increase. In this case, there are also significant barriers to evaluating risk related to invasive species and pathogen introduction because any experimentation in nature would necessitate risky procedures. One remedy is to move coral genes, not colonies, especially if gamete cryopreservation is more

successful in the future. Another option might be to focus on translocation across depths rather than latitude to reduce distance moved, but such closer distances are more likely to be within natural dispersal ranges such that intervention would be less relevant and impactful.

CONTEXT DEPENDENCY OF INTERVENTIONS

In addition to identifying the range of intervention options based on their technical readiness, the committee also recognized that the suitability of either testing or deploying a particular intervention would vary across geographic regions, given differences in the ecological settings and social systems. Here, the committee provides an expert judgement of the attributes that might dictate which interventions are available in a particular jurisdiction, or alternatively, where within the jurisdiction an intervention might be tested or deployed. This evaluation is based on the ecological targets of an intervention and the ecological variables that may be at risk from an intervention (the details of which are described more fully in the committee's first report). This evaluation describes intuitive expectations based on the best-available science, and as such, represents hypotheses that could be evaluated in a model of the type developed in Chapter 4.

The details of the local ecological and social setting in which a particular intervention is either tested or deployed will determine its suitability and/or effectiveness. In some cases, these details could have different implications for interventions based on whether an intervention is being tested or deployed. For example, minimizing risks is a higher priority when testing, while maximizing benefit may be a higher priority when deploying at scale (assuming best practices to reduce risk are developed in the testing phase). Describe here are some of the principal location-specific criteria that might be used to determine where (and in some cases, when) a particular intervention might be considered.

The Biophysical and Ecological Context

Degree of reef degradation: Most interventions will likely target degraded reefs, as indicated by reduced amounts of live coral cover or changed composition (e.g., species or intraspecific genetic diversity), because a high degree of degradation may be needed for an intervention to be warranted. Focusing on highly degraded reefs to test interventions also minimizes risks to more intact reef systems, unless both are part of a connected network of reefs. However, there is a tradeoff: interventions might be less successful on degraded reefs due to the presence of the local stressors that led to reef decline. Interventions on more intact reefs may give higher returns because prevention in combination with restoration increases the chance of producing beneficial outcomes (Possingham et al., 2015). Therefore, a focus on highly degraded reefs to test interventions may help minimize the risks of as-yet-untested interventions. But more intact reefs might be preferred for deployment at scale to maximize the likelihood of success and, therefore, benefits. For example, genetic interventions, particularly genetic manipulation of coral or symbionts, rely on a successfully reproducing population of corals in order to spread. Furthermore, reefs that are currently highly degraded due to historical stress, but which have been recently managed to reduce that stress (e.g., improved water quality, fisheries management, substrate availability, etc.) might represent both a place with lower risk and higher likelihood of success. Areas that contain both high and low levels of reef degradation allow the opportunity to

conduct a comparative approach for testing interventions in both degraded and healthy contexts. Such interventions include managed breeding approaches that require comparing the fitness outcomes across populations.

Disease outbreak: The majority of interventions are best tested or deployed in areas where disease is not active or has not recently impacted the coral population for three reasons. First, the confounding effects of disease are likely to obscure results. Second, some interventions, such as cryopreservation, managed breeding, pre-exposure, or managed relocation, might exacerbate the severity or spread of the disease. Third, interventions that increase stress tolerance (e.g., pre-exposure, managed relocation, or symbiont or microbiome manipulation) might create tradeoffs with disease resistance (Jones and Berkelmans, 2010; Shore-Maggio et al., 2018). Exceptions to this are the disease interventions themselves (e.g., antibiotics and phage therapy), where disease needs to be present to test effectiveness.

Bleaching history and future projections: Most interventions that aim to increase heat tolerance (and thereby reduce the severity of future bleaching events) need to be tested in areas where bleaching has a high probability of occurring in the future to evaluate their efficacy. However, while high past bleaching history can be an indicator of future re-exposure to thermal stress, it might not mean that corals in those areas remain highly susceptible. Prior bleaching events can result in the removal of susceptible coral genotypes, shuffling of symbionts toward more resilient types, and acclimatization that might make interventions less relevant (B. Brown et al., 2000, 2002; Sully et al., 2019). Depending on the severity of past bleaching and the likely future risk of bleaching, these areas might be either considered low priorities for intervention if recent bleaching was severe and projections of future bleaching are low-to-average, or high priorities for intervention if projected future bleaching is high (Figure 2.2). If past bleaching was high and future bleaching is projected to be high such that reefs are both more degraded and less likely to persist into the future, these reefs might even be considered priority sites for intervention because the state of the resource and its future bleaching exposure might indicate that the risks of intervening are minimized. These conundrums suggest that a reliable and comparative way of testing a set of corals for heat tolerance would be an important part of the monitoring toolbox for most interventions.

A combination of historic observations of bleaching, future expectations of bleaching, and testing for heat tolerance could help define the value of local interventions to increase heat tolerance (Figure 2.2). Exceptions to this might include interventions that involve sexual reproduction of healthy individuals (e.g., managed breeding, and gamete and larval capture and seeding). Such reproduction could be hindered if bleaching occurred before the intervention and larval survival might be impaired if bleaching occurred after settlement. Areas with high potential for future bleaching are also candidate areas for shading and cooling environmental interventions.

Water quality: High water quality is generally preferred for most interventions under the expectation that conventional management approaches to maintaining water quality (e.g., reducing nutrients and sedimentation) will help maximize the health and survivorship of corals on which interventions are being implemented. Some interventions that may relate to overall coral health and function, such as manipulation of algal symbionts and the microbiome, may be

appropriate to test across different sites that vary in their water quality to assess how these parameters can influence the success of manipulations. This would then inform the range of acceptable water quality values for deployments designed to maximize intervention success.

		Projected future bleaching	
		Low-to-average	**High**
Recent bleaching history	**Low**	Low exposure: Do not intervene	Susceptible: test and intervene
	High	Possibly pre-adapted: test before intervening	Impacted reefs and high future exposure: Intervene

Figure 2.2 Possible framework for intervention planning as a function of past bleaching history and future bleaching projections.

Herbivory: As with high water quality, high degrees of herbivory (either natural, managed, or enhanced) might maximize the survival of corals on which interventions are implemented by reducing overgrowth and competition by macroalgae (Adam et al., 2015; Ladd et al., 2018). High herbivory may be especially important for interventions that involve the outplanting of recruits and small fragments (e.g., managed breeding, managed relocation, gamete and larval capture and seeding) because of increased coral susceptibility to macroalgal overgrowth at small sizes (Birrell et al., 2008; Box and Mumby, 2007; Martinez et al., 2012), as well as reduced oxygen levels and pH at night close to the substratum due to algal photorespiration. In contrast, low herbivory might be preferred for testing use of nutritional supplementation, to evaluate the impact these interventions have on surrounding nutrient flow and evaluate the risk of their stimulation of algal growth.

Recruitment capacity/substrate availability: Reproductive interventions such as managed breeding and gamete and larval capture and seeding would typically favor testing and deployment at sites with high substrate availability and quality (such as the presence of crustose coralline algae), which impact recruitment capacity. Water quality is also a key parameter as it affects bacteria known to induce larval recruitment in a number of species. Overall, coral recruit settlement and survival depends on the interactive effect of an array of factors including nutrient levels, algal density and composition, and herbivore density and composition (Birrell et al., 2008; Jouffray et al., 2015; J. Smith et al., 2010).

Degree of connectivity: At the testing stage, isolated sites (low connectivity) are preferred for most interventions to reduce widespread unintended consequences. For example, low connectivity areas reduce the spread of nonnative corals, pests, and pathogens, which are all risks associated with managed relocation approaches. Low connectivity also reduces the risk of unintended gene flow. Once testing has led to the development of best practices to reduce risks, then reefs that have high connectivity might be targeted for deployment to maximize the likelihood that benefits of the intervention spread, especially for interventions targeted at genetic

and community composition (e.g., managed selection, managed breeding, gamete and larval capture and seeding, managed relocation). However, low connectivity reefs may benefit most from managed relocation (Hewitt et al., 2011).

Spatial extent of reef: At the testing stage, replicate sets of small patch reefs (with appropriate replicate control patch reefs) might be a good strategy for leaving a smaller intervention footprint and reducing risks for many interventions. However, once testing has led to the development of best practices for reducing risks, then interventions might be deployed at reefs with a larger spatial extent to maximize benefits. A large reef may be optimal for implementing shading and cooling interventions, where a patchwork design for implementation would be possible. Because environmental interventions have the risk of halting natural adaptation and acclimatization processes, leaving some areas unaffected could allow for reproduction between shaded and unshaded (with a higher likelihood of developing thermal tolerance) corals.

Potential for cold shock: At the testing phase, many interventions designed to increase thermal tolerance, such as managed relocation, managed breeding, or pre-exposure, might choose sites based on likelihood of cold shock. If there is the potential for cold shock in individual locations within a region, including such sites in testing will help assess whether an intervention designed to increase high temperature tolerance comes with a decrease in low temperature tolerance, making them vulnerable to cold shock. If this is the case, then sites with low potential for cold shock might be prioritized when deploying at scale to increase the likelihood of intervention success.

Spatial variability in temperature: Several interventions, such as managed breeding or assisted gene flow, require significant thermal variability among sites at both the testing and deployment phase. This is because the standing genetic variation that is the prerequisite for these interventions likely arises in response to long-term differences in thermal regime among sites. Local-scale variability is also an indicator of the presence of genotypes that may be candidates for managed selection.

Select attributes of target species: Different species are likely to have differential success with certain interventions. Specific interventions that may be best used for particular types of species are described here.

- **Managed selection:** Requires predictable gamete or larval release, with hardy larvae.
- **Supportive breeding** and **outcrossing between populations** (managed breeding): Require key reef-building species, especially those with rapid growth traits to increase feasibility of breeding in captivity.
- **Hybridization between species:** Requires an ability for two species to form hybrids, and potentially fertile hybrids, depending on management goals. In most cases, this ability is rare.
- **Gametes and larval capture and seeding:** Best with larvae from species that are fast growing or capable of fusing.
- **Coral genetic manipulation:** Best for species with short generation times to decrease the time needed for testing and proliferation into the population. History of resilience to climate change provides appropriate genetic basis.

- **Symbiont genetic manipulation:** Requires generalist symbiont known to be capable of forming associations with diverse coral species and a known history of conferring thermal tolerance in local reef environment.
- **Algal symbiont manipulation:** Requires coral species with the capacity to maintain stable associations with diverse symbionts.
- **Microbiome manipulation:** Requires coral species with the capacity to maintain stable associations with diverse symbionts.

The Management Context

Infrastructure and resources: Generally, resource requirements are high for testing and deploying most interventions at large scales. However, in some cases this infrastructure may already exist, such as restoration programs that currently propagate corals in nurseries and outplant corals in large numbers. These existing resources provide an opportunity to rapidly test some interventions, and potentially scale these resources up for deployment. Some of the general requirements for the different intervention types are detailed below.

- **Genetic and reproductive interventions** typically require an existing sexual restoration program, including the capability to collect gametes or larvae, rear them in ex situ facilities, and settle them on substrates that can be deployed in the field. This typically requires a combination of in-water boat and dive support, field laboratory, and settlement facilities (either in the laboratory or in nearshore in-water systems). Assisted gene flow and managed selection require test facilities that can measure heat tolerance of individual colonies; map them; and return to them for sampling, propagation, or gamete collection. Different clones show different responses to heat, grow-out location, or other conditions such as disease (Morikawa and Palumbi, 2019; Muller et al., 2018), so these interventions require the ability to label and follow clones over a period of years. Some interventions (e.g., genetic manipulation) require extensive technical expertise to develop methods and protocols that are not currently available, in addition to suitable molecular laboratory facilities, typically only available at large research facilities. For some of these interventions, quarantine facilities for genetically-modified organisms will also be needed to prevent their escape to the wild.
- **Physiological interventions** commonly need existing restoration and monitoring activities (either sexual or asexual) when interventions are performed in a laboratory or nursery setting and then outplanted. They often also require some degree of technical expertise or specialized equipment (e.g., molecular assays or physiological laboratory) to develop the intervention and/or test its effectiveness. Quarantine facilities may also be needed, especially for testing disease interventions such as antibiotics, phage therapy, or probiotics (a form of microbiome manipulation).
- **Population and community interventions** will usually require an existing asexual propagation program, including coral fragment collection, tolerance testing (thermal and disease susceptibility), mapping, labeling, construction of nurseries, and an outplanting and monitoring program (i.e., boat and dive support). Quarantine facilities for non-native species or non-local genotypes (i.e., species or genotypes not normally found in the site or region where the restoration program is located) will also typically be required to reduce the likelihood that they carry non-local pests and pathogens.

- **Environmental interventions** will typically require significant infrastructure that does not already exist at the site of deployment, such as for atmospheric shading or cool-water mixing. However, infrastructural needs for some interventions could be relatively modest, such as mitigation of ocean acidification locally by restoring corals adjacent to seagrass beds (which typically requires infrastructure similar to those for population and community interventions). Reef shading using microfilms (which could deploy a small amount of microfilm over a relatively large area) would require less than most environmental interventions, but nevertheless needs boat deployment, cleanup, and monitoring.

Size of management jurisdiction: The size of the management jurisdiction may need to be relatively large for some environmental interventions, such as atmospheric shading, which are likely to impact large areas rather than target particular reefs. In such cases, impact across national borders might be an important management issue. For other interventions, especially physiological interventions, the size of the jurisdiction is less critical, because the intervention is intended to operate over much smaller scales. Some interventions, such as managed breeding or relocation, may not necessarily require a large jurisdiction, but may instead depend more on cooperation between jurisdictions, including agreements to provide restoration or breeding stock that are more heat tolerant. For the most part, the larger a management jurisdiction, the more intervention options there will be. Large areas might consider zoning certain areas for the testing and deployment of interventions as a way of managing risk. In contrast, smaller jurisdictions may be more responsive to adaptation needs because they have fewer stakeholders and a simpler decision-making structure.

Regional management consensus: As mentioned above, some site-based interventions (such as antibiotic treatment of a coral disease outbreak) may require little consensus between adjacent management jurisdictions in order to proceed, whereas others, such as atmospheric shading, may require a broader management consensus before they can be attempted. Achieving consensus is likely to become increasingly challenging as more jurisdictions are involved, making some interventions much more difficult to test and/or deploy. Determining which jurisdictions have standing in a decision-making process may also be challenging. For example, breeding corals sourced from two different locations to produce offspring that are more thermally tolerant may appear to be a question involving only the jurisdictions that provide the parents, and the jurisdiction that outplants the offspring to the wild. However, other management jurisdictions with connectivity to the outplanting site will also necessarily need to be considered in the decision-making process. Consequently, some common set of guidelines will need to be developed to accommodate these different interests. In general, the higher the level of success of an intervention, and the more broadly it is deployed, the more consensus among regions is required. Multi-jurisdictional consensus is not included explicitly in the decision framework but how these might be reconciled via deliberation when setting multiple objectives and analyzing tradeoffs is discussed.

Societal acceptability: An important consideration regarding whether an intervention can be tested or implemented is the degree of perceived social license granted to a management group to pursue an intervention in the first place. Even if best practices have been developed and can be followed, controversial interventions may not be implemented until the intervention in question

becomes acceptable to stakeholders. Acceptability will most likely be related to the need for interventions, their likely benefits and risks (real and perceived), and steps being taken to minimize risks and maximize benefits whenever interventions are attempted and the efforts made to communicate this to stakeholders. The role of stakeholder engagement in identifying acceptable interventions is described in Chapter 3.

INTERDEPENDENCE AMONG INTERVENTIONS

It is clear that some interventions are highly linked, and that their advantages are not independent. Managers may be in a position of examining multiple interventions (as well as conventional strategies) in combination, and there are possible efficiencies that may arise due to interdependence across interventions. Interdependence can arise from at least three causes: (1) two interventions may use the same infrastructure or raw material, (2) using one intervention might make a second one more or less likely to succeed, or make it more or less costly, and (3) two interventions may benefit from the same research and development programs. The goal in the following is to point out some of the strongest interdependent relationships among interventions. The committee did not exhaustively analyze all possible combinations of interventions from its first report. Instead, through expert judgement the committee identifies cases with clear relationships among interventions in infrastructure, raw material, chance of dual success, and joint development needs.

Related infrastructure: Many interventions need dedicated work space in marine laboratories with good running sea water systems, so that parent, juvenile, or larval corals can be grown. Managed selection, managed breeding (all three kinds), gamete and larval capture and seeding, algal symbiont manipulation, and microbiome manipulation all might be based in such a laboratory setting. As a result, investing in marine laboratory resources would benefit all of these approaches. However, limited seawater space at marine laboratories might lead to competition among proponents of different interventions for laboratory space. As a result, strong deployment of one of these interventions would provide infrastructure that could facilitate the others, but competition for laboratory space might create delays. In situ larval cultivation in open water, can allow the needed scale to be achieved while reducing such competition (Heyward et al., 2002). Likewise, development of genetic tools to alter coral genomes might also generate knowledge, staff, facilities, or bioinformatics tools that would benefit genetic manipulation of symbionts.

Raw material: Some interventions require the raw material of certain coral colonies, larvae, or other biological resources. Some of these similarities could enhance the success of similar interventions. For example, managed breeding (supportive breeding and outcrossing between populations), managed selection, and assisted gene flow all depend on the detection and certification of particular coral colonies as either stress resistant or sensitive. As a result, programs and protocols that find and test coral colonies can provide a boost to all these interventions. Whether these colonies are a limiting resource on native reef habitats or are abundant enough to fuel all the interventions that need them is a question for future mapping studies. “Corals of opportunity” from permitted activities such as dredging, especially from highly stressed areas such as harbors, can contribute to the supply and provide valuable genotypes.

Likewise, interventions that require larvae will jointly benefit from research and facilities that induce coral spawning beyond their often-limited window. Facilities that can deliver larvae weekly, for example, could advance research in outcrossing, hybridization, genetic manipulation, pre-exposure, and algal symbiont manipulation. Access to a wide array of known symbiont cultures, could also advance pre-exposure and algal symbiont manipulation.

Chance of dual success: There are circumstances in which two interventions together could provide strong benefits that are not provided by one alone. In theory, any of the interventions reviewed by the committee could act this way. For example, increasing coral health with nutritional supplementation might make other interventions more successful by decreasing the amount of heat resistance needed. Likewise, deploying environmental interventions that reduce the degree of coral exposure to thermal stress may improve the chances that a thermal tolerance intervention will succeed. However, antagonistic relationships might also occur. For example, the environmental interventions to reduce thermal stress might instead reduce the success of genes or species introduced or promoted in interventions focused on increasing thermal stress tolerance. A key question is whether any of these interventions together have a synergistic or antagonistic effects, where the impact of the two together is greater or less than the sum of the impacts of each alone (where an antagonistic interaction might still lead to a net positive outcome but less than expected from combining independent expectations). A possible example might be that enhanced herbivory within marine protected areas (MPAs) may promote larval settlement of local progeny of transplanted, heat resistant colonies. In such a case, the dual interventions of assisted gene flow and MPA designation may promote resilience better than the sum of either intervention alone.

Capacity building—social as well as infrastructure: The above examples show how infrastructure development can benefit a number of different interventions. Just as important, though, may be social systems at the state or local levels that promote the use of interventions in real-world settings. Simple systems to test corals for heat resistance, grow them in non-laboratory settings, create nurseries that have a variety of species and strains within species, and transplant them out onto reef surfaces would have a strong impact on the ability of well-researched interventions to be deployed to reefs across the world. Development of the ability of non-scientists to contribute effectively to testing and deploying interventions is a key area that would require a focus on education, citizen science, and the kind of help that might resemble best the knowledge transfer systems on which local application depends. The training of more culturally-connected local scientists from coral reef jurisdictions is also an important undertaking for local capacity development.

Conclusion: Multiple, inter-related interventions provide a toolbox for increasing coral reef persistence and resilience. This set of options can be tested and deployed based on community goals, ecological objectives for reef management, and the benefits and risks across multijurisdictional or even multinational boundaries. These efforts are likely to evolve over time as interventions become more feasible and as new interventions are developed.

3
Best Practices for Developing Structured Decision Support Systems for Coral Interventions

The decision to implement one or more interventions to support coral resilience under global environmental change exists within a broader decision context, where multiple natural and human driving forces, pressures, environmental states, and environmental and management responses interact. Therefore, such a decision should be made with consideration of other (local) stressors (e.g., poor water quality), a suite of management programs and restoration activities (e.g., management of these local stressors), and a range of human values. Within this decision context, there are likely to be multiple and potentially conflicting stakeholder objectives. Additionally, there will be uncertainty about system dynamics, future conditions, and the risks and benefits of a particular decision. Different management activities, including the use of coral interventions, will vary in risk and uncertainty and in their ability to achieve defined objectives. Decision support tools and best practices exist to guide the evaluation of tradeoffs in achieving various management objectives that can be expected given the state of knowledge. An adaptive decision approach provides a structured framework for evaluating potential management actions using an iterative process that allows for continuous learning about the linked human-natural system and improvement of management decisions. The use of a decision support framework that integrates an adaptive management process requires stakeholder engagement, data collection and monitoring, and modeling efforts, but is an investment that pays off with a prioritized set of coordinated, comprehensive, scientifically-driven, and long-term strategies to achieve long- and short-term goals.

The goal of this chapter is to provide an overview of best practices for structured decision making, including high-level descriptions of specific decision analytic approaches useful for evaluating the consequences and tradeoffs arising from implementing particular coral interventions. An array of approaches and tools are available, the suitability of their use being dependent on local conditions, resources, or state of knowledge. Many of these tools have been implemented in coral reef decision contexts, and example situations have been highlighted in this chapter. Though typically implementation of these tools has been limited to management of local stressors, they have utility for evaluating coral interventions as part of an overall management strategy.

DECISION SUPPORT CONTEXT OF CORAL INTERVENTIONS

Coral reef management is dynamic and complex, and the expectation is that a number of different actions will be required across temporal and spatial scales as coral reefs respond to multiple human pressures and deteriorating environmental conditions. As environmental conditions change, local reef managers and decision makers will benefit from access to new interventions that have the potential to increase the persistence and resilience of coral reefs in the face of increased thermal stress, ocean acidification, and potential disease outbreaks.

Additionally, the intervention landscape itself is highly dynamic as new technologies and approaches are developed, tested, and better understood, continually providing new and improved management options. While it may be tempting to think these interventions can be evaluated and implemented in isolation, it is important to address the effects of traditional stressors (e.g., contaminant loadings, fishing pressures, water quality), which will influence the probability of intervention success due to the complex interactions across attributes of the coral reef ecosystem.

The DPSIR (Drivers—Pressures—State—Impact—Response) framework (Atkins et al., 2011; Kelble et al., 2013; Rehr et al., 2012) provides a useful organizing framework for structured decision making (Figure 3.1) by linking socioeconomic factors and human activities with changes in biophysical metrics of coral reef health associated with declines or improvements in ecosystem services. The DPSIR framework provides a structure for integrating environmental and socioeconomic relationships, understanding of which is developed based on monitoring data, analytical studies, predictive models, expert judgment, and other studies. Driving forces are the socioeconomic and cultural factors leading to the human activities that in turn create pressures on coral reefs. These will range from local drivers such as tourism and coastal land development to the global drivers contributing to climate change. The resulting pressures include local inputs of pollutants, as well as thermal stress and ocean acidification. The pressures result in degraded environmental states and coral reef condition. The impact of that degradation is a decrease in ecosystem services and the benefits provided by coral reefs to local communities. Finally, there are a set of responses, or management alternatives, that are directed at improving the state of coral reefs by affecting the pressures on, or state of the reef. These alternatives will have differing impacts on coral reef condition. The DPSIR framework can be used as a tool for establishing the decision context with stakeholders as described in Step 1 of the process outlined in this chapter (as seen in Bradley and Yee, 2015; Yee et al., 2015).

A STRUCTURED, ADAPTIVE APPROACH TO DECISION MAKING

Structured decision making is a deliberative process for evaluating how a set of alternatives can best achieve stakeholder and decision maker objectives by maximizing benefits and minimizing potential risks (Gregory et al., 2012). It guides the management responses within the larger landscape depicted in the DPSIR framework. Effective decision making under uncertainty benefits from an adaptive and structured decision-making strategy as shown in Figure 3.2 by allowing for an iterative process of planning, acting, evaluating, and responding over dynamic spatial and temporal scales. Adaptive management consists of planning, evaluating options, establishing monitoring goals, and iteratively adjusting management plans depending on the continuing evaluation of changes in coral reef function, structure, and health (Holling, 1973; Walters, 1986; Walters and Holling, 1990). Figure 3.2 is nested in Figure 3.1 to reflect the focused decision landscape necessary to compare potential responses and interventions within a broader management context.

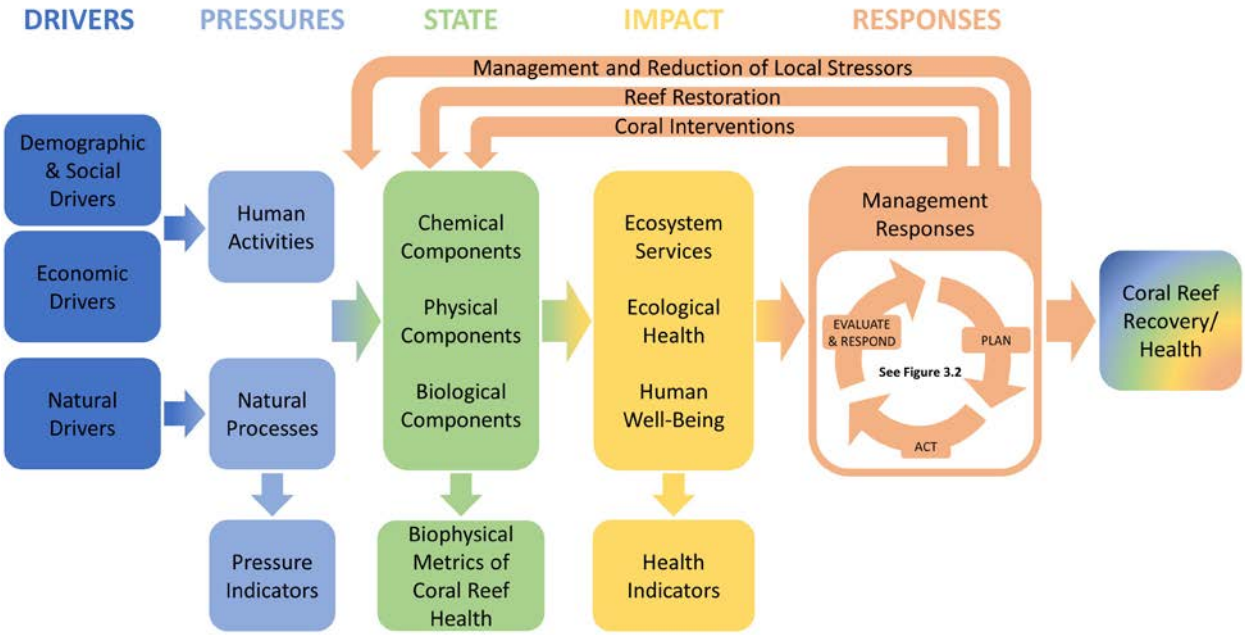


Figure 3.1 A DPSIR (Drivers—Pressures—State—Impact—Response) framework that integrates the implementation of coral interventions into the management context. The arrows within the figure represent the feedback between management responses and the pressures, stressors, and environmental condition. The iterative nature of management responses is depicted in detail in Figure 3.2. SOURCE: adapted from Harwell et al., 2019

A strength of the structured decision-making approach is the focus on eliciting objectives, decision criteria weights, and evaluation metrics from a variety of stakeholders who may have fundamental disagreements around management of a shared resource. Decisions made on the basis of "intuition" or "gut feelings" may not reflect the complete underlying values of diverse stakeholders or objective functions of decision makers (Addison et al., 2013; Hammond et al., 1999; Howard, 1988; Keeney and Raiffa, 1993; Runge, 2011). Structured decision making provides a way to compare different attributes and outcomes across potential alternatives in a consistent way, and standardizes disparate quantitative and qualitative outcomes that are difficult to compare otherwise. The first step in any structured decision-making process is problem formulation to establish the scale of the decision context, and specific objectives, regulatory landscape, and array of stakeholders to be involved in the process (e.g., Gregory et al., 2012; Runge, 2011). The localized context of this first step is the primary reason why prescriptive, externally developed approaches are rarely useful, let alone successful.

The process of developing a decision framework can be as important an accomplishment as the application of the framework to evaluate alternatives. For example, Fletcher et al. (2015) conducted a needs assessment survey with coral reef managers to identify data needs around the relationship between climate change and coral reef health, and how those might best support the development of prototype decision-support tools. The study was conducted over nearly five years with the result that the median rating by participants around a set of climate tools was only 3 (moderately useful) out of a scale of 1 to 5 (not useful to extremely useful). This was even after completing a tutorial around each of the climate tools. This exercise highlights that the

application of structured decision-making approaches typically requires facilitation and engagement. Whereas the decision tools themselves are useful, it is the engagement involving people that produces solutions. The structured decision-making process itself can be used as a two-way process whereby the decision analysts and system modelers learn from stakeholders and decision makers, and decision makers and stakeholders gain new clarity around what options they have available and what choice of strategy might deliver the greatest benefits at minimal risks given multiple objectives and value preferences.

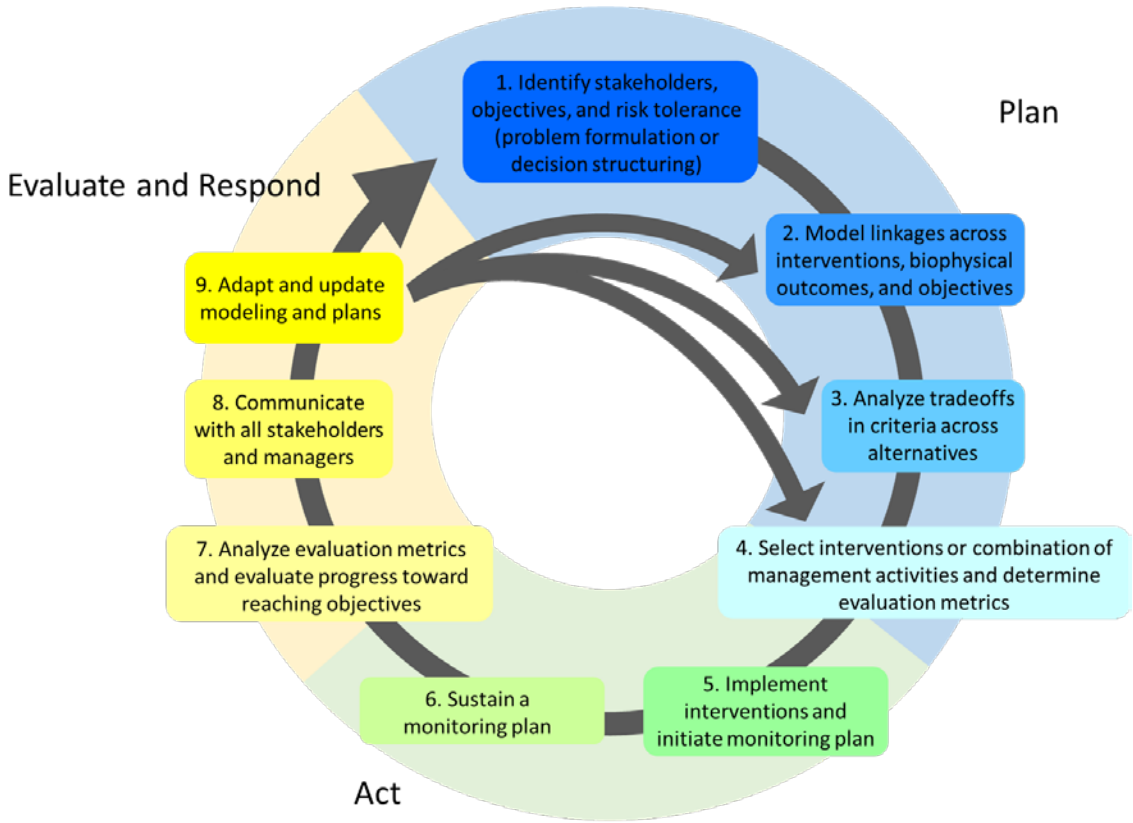


Figure 3.2 The adaptive management cycle shown as three major phases (Plan, Act, and Evaluate and Respond) composed of nine steps. The arrows connecting step nine (Adapt) to steps two, three, and four demonstrate the iterative nature of this management approach. SOURCE: adapted from Delta Stewardship Council, 2013.

Step 1: Identify stakeholders, objectives, and risk tolerance (problem formulation or decision structuring)

The decision context includes long- and short-term goals; ecological, economic, and social objectives (defined and measurable strategies or steps to meet these goals); and decision criteria. Problem formulation, or decision structuring, is the process of transitioning from a vague articulation of a poorly-defined problem by decision makers and stakeholders to a clear definition with an associated analysis framework (von Winterfeldt and Edwards, 2007). Each stage of the adaptive management process involves interaction and collaboration among decision makers, stakeholders, scientists, and decision analysts. It is in this first problem formulation

stage that these key actors and their roles are identified. Although decision makers have primary responsibility for problem formulation, stakeholder preferences are required to establish goals and objectives that will lead to the criteria against which interventions will be evaluated. Scientists and coral reef ecologists will have insight into local conditions from a biophysical and ecological perspective. Local scientific knowledge will be required to develop predictive models of how the ecosystem (and linked social system) might respond to interventions (consequences), to contribute to the identification of critical uncertainties. Local knowledge, in collaboration with stakeholders, may also establish appropriate and targeted monitoring programs that can help assess the performance of interventions against established criteria (e.g., Nichols and Williams, 2006) and provide early warning for where an intervention might be critically needed (Dale and Beyeler, 2001). Environmental and ecological consequences then need to be translated to impacts on ecosystem services and values for people to inform how different strategy options affect multiple objectives. Problem formulation formalizes a shared understanding of the policy, legal, ecological, social, and economic drivers and how they give rise to the specific decision-making context.

The U.S. Environmental Protection Agency's (U.S. EPA) Coral Reef Protection Plan has a goal of reducing anthropogenic stress on Caribbean coral reefs by promoting institutional practices that improve reef condition and directing regulatory and non-regulatory decision making toward minimizing contaminant releases to coastal systems (described in Carriger et al., 2018). Although the Coral Reef Protection Plan emphasizes conventional contaminants and stressors, it provides a good example of structuring management objectives, sub-objectives, and attributes to carry through the entire adaptive management process. Table 3.1 shows the relevant objectives identified for the Coral Reef Protection Plan based on a series of stakeholder/decision maker engagement meetings. Identifying the overall objectives and potential associated metrics (identified as sub-objectives 1 and 2 in Table 3.1) are critical to establishing stakeholder priorities, selecting which interventions might be appropriate for further consideration in a decision framework, and identifying the boundaries of the decision. Failure to reach consensus (or at least reconcile different views) on what is important can lead to failure of any intervention or restoration program.

Given that coral reef ecosystems provide a suite of services that translate to benefits and values for society (e.g., Costanza et al., 2014; Stoeckl et al., 2011), the ecosystem services provided by the reef in question will impact the risk tolerance across stakeholders and decision makers and their willingness to trade off between key values. The ecosystem services generated by coral reefs will vary from system to system both from a biophysical perspective as well as with respect to stakeholder values (e.g., Hicks et al., 2015). The U.S. EPA and others have developed assessments of ecosystem services derived from coral reefs worldwide (Brander et al., 2013; Principe et al., 2011), identifying at least 30 individual ecosystem services ranging from direct extractive uses (e.g., fishing) to direct nonextractive uses (e.g., recreational activities such as diving). These services also encompass indirect uses (e.g., reduced flooding, fish habitat) and nonuse values (e.g., existence value). The specific values that stakeholders and decision makers place on ecosystem services generated by coral reefs will be context-specific and are likely to vary both spatially and temporally.

Table 3.1 Coral reef protection objectives identified by the U.S. EPA based on stakeholder meetings for the Coral Reef Protection Plan.

Category	Fundamental Objective	Sub-objective 1	Sub-objective 2
Environmental	Protect, restore, and enhance ecological integrity of coral reef systems	Individual coral colonies Coral reef communities	Endangered or threatened colonies Non-endangered nor threatened colonies
Economic	Protect, restore, and enhance economic benefits from coral reef systems	Property protection from storm waves Economic benefits from reef related activities	Tourism/visitation Fisheries
Social	Increase employment in reef-related industries Protect, restore and enhance social benefits from coral reef systems	Traditional uses of reef resources Recreational benefits	Availability of coral fish species and resources for traditional uses (e.g., festivals, local markets) Traditional fishing and harvesting of reef resources
Human health	Protect, restore, and enhance human health benefits from coral reef systems	Protection of human lives from storm waves Sustenance from fisheries species Pharmaceutical discoveries	Mortality from storm waves Morbidity from storm waves
Governance/Political Commitments	Foster long-term public support and trust		

SOURCE: Recreated from Carriger et al., 2018.

Stakeholder and decision-maker tolerance and acceptance of intervention risks is another important attribute that will influence the evaluation of which intervention or set of interventions to try at which time. For example, stakeholders may express a higher tolerance for risks associated with largely untested interventions if a reef is considerably more degraded (see Chapter 2 for a discussion of such context dependencies). These values are only revealed through a transparent decision-making process combined with active stakeholder engagement (Anthony et al., 2017; Kaebnick et al., 2017).

A variety of tools and approaches exist to facilitate setting up problem formulation or what has also been called decision structuring, including means-ends diagrams, objectives hierarchies, and value trees (see, for example, von Winterfeldt and Edwards, 2007 for a lengthy discussion of decision structuring; also www.structureddecisionmaking.org). These are largely graphical methods that link actors, actions, and objectives, and are used to identify the key underlying issues, select an appropriate analytical approach, and refine the analysis structure.

Step 2: Model linkages across interventions, biophysical outcomes, and objectives

Any proposed intervention will lead to biophysical consequences and changes in environmental states and coral reef condition. The impacts of interventions may occur at different scales from the scales at which interventions are applied. It is critical to model, as quantitatively as possible, the range of biophysical (and as appropriate, social or economic) consequences or possible environmental states predicted to occur as a result of an intervention or set of interventions. Models design and input parameters should be tailored to specific locations at relevant spatial and temporal scales. Biophysical models should assume that coral reef systems are dynamic and characterized by stochastic variability, and that there is uncertainty in knowledge about these dynamics. Biophysical outputs can include such attributes as coral growth and cover over time, coral diversity, herbivore biomass, coral disease, macroalgae cover, and other metrics identified by researchers, stakeholders, and decision-makers as critical indicators of coral reef health and resilience (e.g., Anthony et al., 2015; Maynard et al., 2017; McClanahan et al., 2012). Chapter 4 provides a simplified example of the kind of biophysical modeling required to predict environmental states as a consequence of implementation of one or more interventions. Developing this critical component of any decision framework requires an understanding of the potential effects and impacts of the intervention. The goal is to identify which proposed set of interventions will deliver anticipated maximum benefits at minimum risks and costs, and what research and development might be required to reduce critical uncertainty and further improve strategy options.

Table 3.2 provides an overview of the most common biophysical models used to assess coral reef condition. A critical first step in the development of a quantitative model or set of quantitative models is constructing a conceptual model of coral reef interactions. This conceptual understanding of reef dynamics is critical for identifying relationships between variables driving biophysical outcomes, including feedback loops. Once the qualitative relationships and interactions have been articulated, then it is possible to determine the mathematical relationships that will quantify those interactions. This could be an equation or a set of equations, and there may already be existing modeling frameworks from the peer-reviewed literature and elsewhere that can provide a starting point, as shown in Table 3.2.

The exact form of the functional relationships between intervention implementation and environmental states or biophysical outcomes will be context- and location-specific. Those relationships are used to define one or more quantitative metric(s) against which to evaluate intervention success. Given that some of the interventions presented in Table 1.1 may be untested at field scale, it is important to note that, in many cases, the risks and impacts of intervention implementation will be poorly understood and therefore difficult to constrain in a modeling context. There may be high uncertainty around risks and benefits of untested interventions, and further, around how they might perform under different climate change scenarios. Chapter 4 provides a highly simplified proof-of-concept example that clearly demonstrates this, but also demonstrates the utility of decision analytic approaches in situations of high uncertainty through likelihood-based calculations under different contexts.

Oceanographic models translate oceanographic or climatological data across locations and through time (Figure 3.3a) into projected outcomes for coral reefs (Figure 3.3b), such as

Table 3.2 A Summary of Common Coral Biophysical Models

Model Type	Brief Description	Examples
Oceanographic (stress-based) models (Figure 3.3b)	Translates environmental dynamics, such as the expected frequency of bleaching events, into predictors of coral demographics such as persistence or connectivity	Donner, 2009; Logan et al., 2014; Wood et al. 2016
Population genetic models (Figure 3.3f,g)	Captures evolutionary change in traits, such as thermal tolerance, as it depends on the fitness (survival and reproductive success) of different genotypes under changing environmental conditions	Baskett et al., 2009; Bay et al., 2017
Physiological models (Figure 3.3h)	Follows physiological dynamics of energetic exchange between a coral host, symbiotic algae, and the microbiome (e.g., dynamic energy budget models)	Cunning et al., 2017; Muller et al., 2009
Stage-structured population models (i.e., matrix models; Figure 3.3e)	Follows the population size distributed amongst discrete stages such as ages or size classes, where demographic rates (growth, reproduction, mortality) depend on stage	Edmunds and Elahi, 2007; Fong and Glynn, 1998; Hughes and Tanner, 2000
Integral projection population models (Figure 3.3d)	Follows the population size distributed over a continuous state such as size, where demographic rates (growth, reproduction, mortality) are a function of state and can depend on the physical and chemical environment	Edmunds et al., 2014a; Madin et al., 2012
Individual-based simulations	Captures demographic stochasticity by following individual-by-individual state and demographic transitions (growth, reproduction, mortality)	Langmead and Shephard, 2004; Mumby, 2006; Mumby et al., 2006
Community models (Figure 3.3c)	Can follow the dynamics of multiple coral species or types as well as additional tropical reef taxa such as algae and herbivores	Blackwood et al., 2011; Fung et al., 2011; Melbourne-Thomas et al., 2014
Combined models	Can combine any of the elements above (stage structure, evolutionary change, multiple species in a community)	Baskett et al., 2010; Riegl and Purkis, 2009;

temperature into bleaching frequency (e.g., Donner, 2009; Logan et al., 2014) or ocean acidification into the capacity for coral calcification (e.g., Hoegh-Guldberg et al., 2007). Oceanographic models can represent the expected spatial scale of anticipated benefits of physical interventions (e.g., shading, mixing of cool water) and associated risks that relate to environmental modification. Oceanographic models that incorporate larval properties (e.g., anticipated release locations and timing, larval duration) can indicate expected connectivity between locations (e.g., Riginos, 2018; Wood et al., 2016), which can inform the expected extent of benefits and risks from interventions as they depend on location (e.g., Hock et al., 2017).

Population genetic models (Figure 3.3f,g) can account for the risks and benefits associated with interventions that affect evolutionary dynamics. Such effects include the benefits of increasing stress-tolerant genotypes in assisted gene flow and managed selection, the benefits of genetic diversity and the combinations of different genotypes in managed breeding, or the risks of missed evolutionary opportunities in stress-reduction interventions such as shading and mixing of cool water. Depending on the focal stressor targeted by intervention, the evolving trait(s)

might be thermal tolerance, ocean acidification tolerance, or disease resistance. Evolution of such traits might occur in different components of the coral holobiont (e.g., symbionts: Baskett et al., 2009; coral host: Bay et al., 2017). The genetic representation can take many forms, from frequencies of individual genes (which can account for the role of drift relevant to the risks and benefits of managed breeding; Figure 3.3g) to trait distributions (Day, 2005; Turelli and Barton, 1994; Figure 3.3f).

Physiological models (Figure 3.3h) such as dynamic energy budget models (e.g., Cunning et al., 2017; Muller et al., 2009) can account for the risks and benefits associated with interventions that affect coral energetics (e.g., antioxidants, nutritional supplementation). For example, a model that mechanistically connects nutrient levels (C, N, and P) to both coral and macroalgal dynamics can assess both enhanced macroalgal growth (with the associated risk of overgrowing corals as described in Fung et al., 2011; Mumby et al., 2007) and the benefit of increased energetic competence (and hence stress resilience) from nutrient supplementation to corals (Connolly et al., 2012). Physiological models can also separate the energetic contributions of different components of the holobiont (coral host, symbiotic algae, and the rest of the microbiome), which is particularly relevant to mechanistically representing interventions that target a particular component of the holobiont (e.g., algal symbiont or microbiome manipulation).

Structured population models (Figure 3.3d,e) are models that follow population size distributed among ages, sizes, or stages such as juveniles and adults. They can account for the risks and benefits associated with interventions that affect the coral demographic processes of growth, reproduction, and mortality. Coral age and size can significantly influence demography and stress susceptibility (Connolly and Muko, 2003), which in turn determines overall dynamics (Hughes, 1984). A common demographic benefit to several interventions is the addition of recruits or small fragments (e.g., managed breeding, assisted gene flow, gamete and larval capture and seeding, managed relocation). Models that account for population structure (e.g., Baskett et al., 2010; Riegl and Purkis, 2009), where recruits can provide significant contribution to the population size, tend to find greater sensitivity to recruitment than models that follow proportion cover (e.g., Edmunds et al., 2014b; Fabina et al., 2015), where recruits add a small amount to overall cover. In addition to more accurately assessing the potential benefits of added recruits, structured population models can help evaluate stage- or size-dependent decisions (e.g., the relative efficacy of moving gametes versus fragments in managed relocation). Structured population models can also be particularly relevant to interventions that affect ocean acidification levels (whether abiotic or biotic) given their ability to capture ocean-acidification-dependent growth and survival on overall population dynamics (e.g., Madin et al., 2012). As with genetic models, structured population models can range from following discrete age or stage classes (matrix models, e.g., Edmunds and Elahi, 2007; Figure 3.3e) to following size or other continuous-state distributions (integral projection models, e.g., Madin et al., 2012; Figure 3.3d).

Community models (Figure 3.3c) can account for the risks and benefits associated with interventions that might affect taxa beyond corals, such as macroalgal dynamics (e.g., nutrient addition, macroalgal beds to reduce ocean acidification). A common modeling framework, explored as an example in Chapter 4, is to incorporate both coral and macroalgal dynamics with

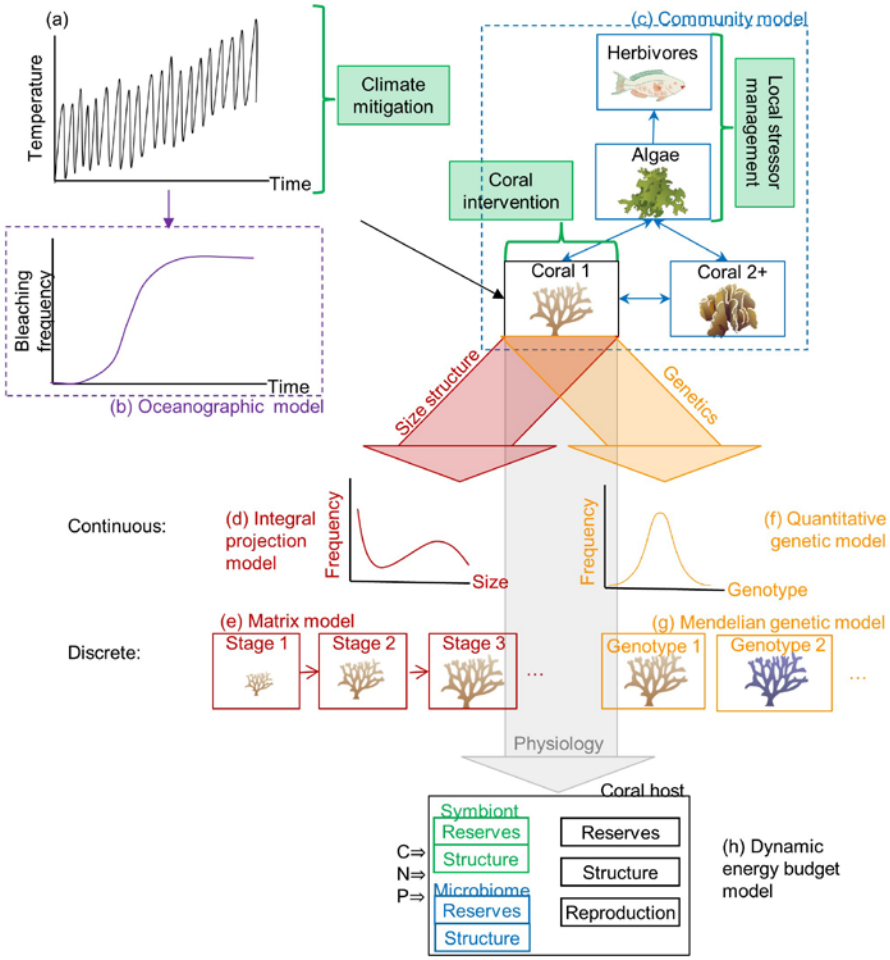


Figure 3.3 A representation of how different model types inform understanding of coral health and are used to make quantitative predictions of biophysical outcomes across different interventions. Filled green boxes with brackets indicate components that depend on policy context or management decisions. Boxes with solid outlines (unfilled) indicate typical state variables, such as coral or coral reef components that change in time, for each model type.

implicit herbivory (i.e., herbivory rate as a function of coral cover rather than following herbivores as one of the changing populations in time; e.g., Anthony et al., 2011; Mumby et al., 2007). Extensions might incorporate explicit herbivore dynamics (e.g., Blackwood et al., 2012) or sensitivity to different functional forms of the feedback between coral cover and grazing (e.g., McManus et al., 2018). Accounting for herbivore dynamics might be particularly relevant if management considerations include fisheries management in conjunction with coral interventions. Community models can also consider multiple coral species, which might be particularly relevant to interventions focused on community-level manipulation (e.g., managed relocation – assisted migration and introduction to new areas). Models with multiple coral species can elucidate the role of coral diversity in reef resilience (e.g., Baskett et al., 2014) and therefore the risks and benefits of focusing interventions on a single target coral species as compared to multiple species in a community. For interventions that affect disease susceptibility and prevalence (e.g., antibiotics, phage therapy, managed relocation), an additional component to

consider modeling explicitly is disease dynamics, such as through susceptible-infected-recovered (SIR) models.

Figure 3.3 provides an overview of these modeling types. The models included here focus on different model types across ecological scales (physiological, genetic, population, community) given that Table 1.1 and the committee's first report (NASEM, 2019) organized the interventions by the ecological scale and process affected. The list of model options inevitably provides a subset of possible dynamics to consider, depending on the local context, and any modeling framework might incorporate more than one of the models. For example, biophysical models of larval dispersal between locations (or other information, such as genetic distance, that can provide anticipated connectivity; Beger et al., 2018) in combination with genetic or structured population models that include recruitment dynamics (e.g., Condie et al., 2018; Kool et al., 2010) can reveal when connectivity-enhancing interventions (e.g., assisted gene flow, assisted migration) are likely to provide benefits beyond what one might expect from natural dispersal. In addition, individual-based simulations of any of the above-described dynamics (e.g., Mumby, 2006 for an individual-based simulation that has both structured population and community dynamics) can account for the role of demographic stochasticity. Furthermore, beyond biophysical considerations, models might account for coupled socio-ecological dynamics (e.g., Thampi et al., 2018). As with any modeling exercise, it is possible to continually add realism to the model structure, which will trade off with model generality, manageability, and increased parameter uncertainty (Levins, 1966; May, 2004). A focus on capturing the dynamics essential to the central risks and benefits to the set of interventions under consideration can help identify the simplest possible model relevant to the decision-making process.

Each modeling framework has unique data needs for parameterization, dependent on the ecological, spatial, and temporal scales of the dynamics modeled. Across ecological scales, data needs will include selection strength and trait-based genetic variation for genetic models, nutrient uptake and assimilation rates in physiological models, demographic rates in structured population models, and species interaction rates in community models. One resource for such parameters is the Coral Traits Database (Madin et al., 2016). The temporal scales necessary to measure these biotic parameters will depend on the time scale of the associated process, from daily for physiological responses, to annually for demographic processes, to generationally for genetic processes. Across spatial scales, data needs might range from local-scale environmental heterogeneity in stressors (e.g., temperature, pH) to basin-scale processes such as larval connectivity; the relevant spatial scale and associated processes to consider depend on the scale of the intervention and associated risks and benefits. Given inevitable parameter uncertainty, sensitivity analysis is a crucial component of model analyses as detailed below.

Any biophysical model of coral reef health and potential response to interventions is an inevitably imperfect representation of reality. Following good model development practices using established guidelines will increase stakeholder and decision maker confidence in model projections used to evaluate potential interventions and management alternatives (for details see Crout et al., 2008; Jakeman et al., 2006; NRC, 2007, 2012; U.S. EPA, 2009). Best practices include the following (from U.S. EPA, 2009):

- Proper definition of scope and objectives of the model: The scale and complexity of models are tailored to the management problem and objectives. Hypotheses underlying the model should be tested.
- Stakeholder participation in model development: Model developers, decision makers, and model users collaborate to specify the problem and objectives to inform and develop the associated model framework.
- Conceptualizing the system: Each element of the conceptual model is clearly described (including as functional expressions, diagrams, and graphs), and the utility and science behind each element is clearly documented.

These are largely addressed in Step 1 of the adaptive management cycle. Best practices for model development also call for an iterative verification-validation-sensitivity/uncertainty analysis to provide decision makers and stakeholders with confidence that the biophysical models are fit-for-purpose.

Verification is the process of determining how accurately the mathematical equations are coded, including code verification (e.g., determining whether the code correctly implements the intended algorithms) and solution verification (e.g., satisfactory reproduction of coral reef behavior or comparison to measured results such as hindcasting or predicting previously observed trends and measurements) (NRC, 2012).

Validation is the process of determining the degree to which a model is an accurate representation of coral reef interactions relevant to the intended uses of the model (NRC, 2012). Cross-validation increases the confidence of model projections by evaluating the consistency of model inputs and outputs by splitting the data set and comparing one half against the other.

Sensitivity and Uncertainty Analyses. Sensitivity analysis is the process of identifying how model projections change as a function of model inputs. Sensitivity analysis can be local—changing one input at a time by a specific amount and recording the change in model projections; or global—using a probabilistic or other type of framework to evaluate model sensitivity to all inputs simultaneously and thereby incorporating dependencies, feedbacks, and correlations (Cariboni et al., 2007). Uncertainty analysis, which is related but different, quantifies the uncertainties associated with model inputs. The goal of uncertainty analysis is to account for all sources of uncertainty and quantify the contributions of specific sources to the overall magnitude of the model output. The source of uncertainty can be in both the model inputs and the model structure. If model projections are highly sensitive to uncertain inputs, it may warrant obtaining further information and data to reduce the uncertainty prior to making a decision. There are formal methods available for more rigorously evaluating how much additional data should be collected in terms of cost versus benefit, for example, using value of information (Comte and Pendleton, 2018; Conroy and Peterson, 2013). Alternatively, it may not be possible to reduce the uncertainty, which might suggest using a probabilistic framework such as Bayesian networks (described in Step 3), although note that Bayesian networks are also extremely useful for quantifiable uncertainty precisely because they are probabilistic.

The proposed interventions are largely untested at scale, as discussed in Chapter 2. This may mean that we do not know and have no way of knowing all the possible near-term effects and

further downstream effects of implementing an intervention. There are likely to be interactions across interventions (some which may be unintended), and the presence and management of local stressors will also influence the probability of intervention success. In principle, high uncertainty can be quantitatively incorporated into most models, but presumes we know what we don't know (i.e., that we can quantify our uncertainty). If the uncertainty cannot be quantified, it is still possible to construct different scenarios, or to use probabilistic modeling approaches diagnostically to answer questions such as "how high or low would the probability of a particular intermediate outcome need to be in order to push the decision one way or the other?"

Expert elicitation is a formal process for using expert opinion to reduce or quantify uncertainty in model inputs (Hemming et al., 2017). For example, Ban et al. (2014) used expert elicitation to develop estimates about the interactive effects of multiple stressors on the Great Barrier Reef, effects for which there is limited data. There was stronger consensus about certain stressor effects (such as between temperature anomalies and bleaching) and weaker consensus on others (such as the relationship between water quality and coral cover).

Example sensitivity analysis:

Thampi et al. (2018) developed a mathematical model of coupled socio-ecological interactions, where human systems and reef systems are both represented dynamically in order to model their influence on each other, to evaluate coral reef cover in a Caribbean coral reef system. These authors developed a series of parameter planes to evaluate model sensitivity under changes in two different model parameters as shown in Figure 3.4. The plane has a model parameter on each axis, and shows the dynamics related to coral health outcomes that occur for each possible pair of parameter values while holding all other parameters at fixed baseline values. Figure 3.4a plots the strength of injunctive social norms (φ) against the parrotfish growth rate (s), while Figure 3.4b plots human sensitivity to coral reef rarity (J) and the maximal fishing rate (σ), again, while

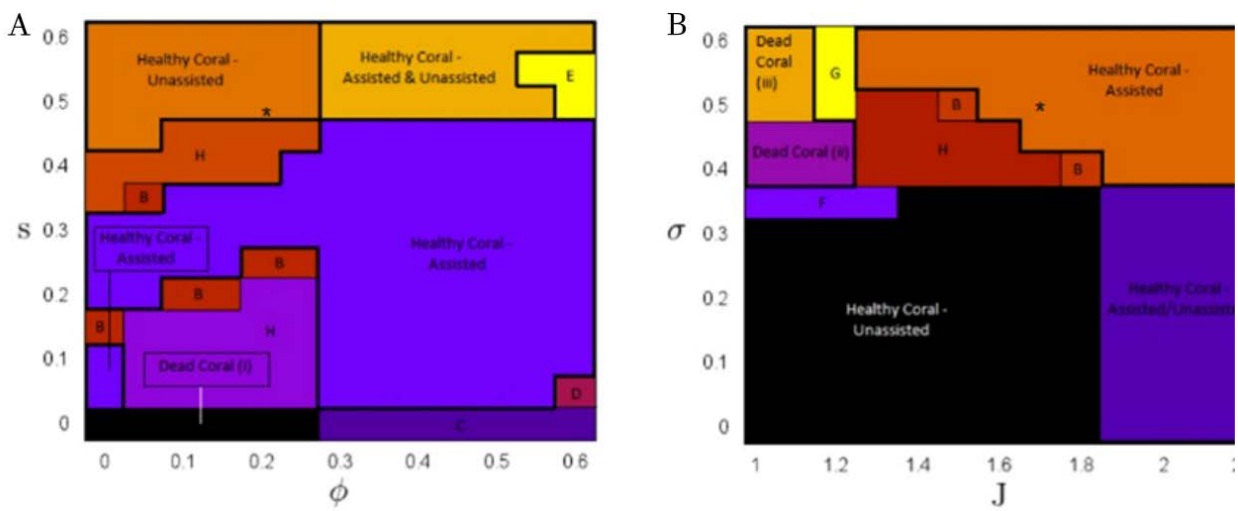


Figure 3.4 Evaluation of the impact of changes in two model parameters (the x- and y- axes) on model results (the coral states represented by different colored block areas). In this example, panel (a) plots the strength of injunctive social norms (φ) against the parrotfish growth rate (s). Panel (b) plots human sensitivity to coral reef rarity (J) and the maximal fishing rate (σ). SOURCE: Thampi et al., 2018.

holding all other model inputs at baseline values. This is only one of many ways of conducting and presenting the results of a sensitivity analysis.

Step 3: Analyze tradeoffs in criteria across alternatives

Reef managers are likely to consider a range of management alternatives, including using one or more interventions in concert with conventional restoration activities as well as taking no action. These combinations, along with uncertainty in knowledge about the reef system and future environment, will yield a range of predicted changes across alternatives with tradeoffs in their abilities to meet management objectives and minimize risk. For example, some intervention strategies may support the growth of a small subset of coral species that provide fish habitat but not the solid reef structure that is needed to provide coastal protection from storm waves. If fish habitat and strong reef structure are both key objectives for different stakeholder groups, then tradeoffs need to be made to reconcile different priorities or value preferences. Additionally, as the impacts of climate change progress, the capacity for management alternatives, including both conventional management and the new interventions, to meet some objectives (e.g., biodiversity or persistence of sensitive species or reefs) may diminish, and will hence drive a need to prioritize among values and places (Anthony, 2016).

Table 3.3 Frameworks for evaluating management tradeoffs

Framework	Description	Examples
Multi criteria decision analysis (MCDA)	Alternatives analysis; specify alternatives, objective function(s), criteria	K. Brown et al., 2001
Decision trees	Probabilistic representation of outcomes; can backcalculate the optimum strategy	Flower et al., 2017; van Oppen et al., 2017
System dynamics models	Systems-based modeling approaches; typically deterministic but time-varying; capture feedback loops	Chang et al., 2008; Rocha, 2010
Bayesian networks (BN) or Bayesian belief networks (BBN)	Models based on conditional probabilities; acyclic (e.g., no feedback loops)	Ban et al., 2014; Renken and Mumby, 2009; Chapter 4 of this report

It is important to introduce tradeoffs early in the structured decision-making process because they are closely tied to the setting of objectives and to value preferences. Early reconciliation of tradeoffs can help guide strategy generation, but they also need to be revisited late in the process once the performance of different strategy options are compared (Gregory et al., 2012; Hammond et al., 1999). All decisions involve evaluating and making tradeoffs and prioritization under uncertainty and resource limitations (Bottrill et al., 2008; McDonald-Madden et al., 2008; Wilson and Law, 2016). This step integrates the predicted changes in biophysical outcomes with other decision-making criteria to evaluate tradeoffs in risks and benefits across potential management activities and interventions. The approach can be as simple as mapping results (i.e., performance metrics) against different objectives (ecological, economic, and social) for each intervention strategy in a consequence table (Groves and Game, 2016; Hammond et al., 1999). This can help managers illustrate to stakeholders which intervention strategy performs better or worse against different objectives, and can inform discussion around which objectives to prioritize. Further complexity can be added through assignments of weights for different values impacted by interventions, which can help managers and stakeholders arrive at a preferred

intervention strategy. There are a number of different frameworks available for evaluating alternatives to assist in determining the optimal course of action (Table 3.3).

Multi-Criteria Decision Analysis

Multi-Criteria Decision Analysis (MCDA) supports complex decision making by explicitly incorporating multiple and potentially conflicting criteria valued differently by stakeholder groups and/or decision makers. Weighted criteria are used as the basis for evaluating tradeoffs across alternatives, which will differ across interventions. In the MCDA framework, evaluation criteria will include, at a minimum, the biophysical outcomes resulting from underlying models. Figure 3.5 provides a schematic of a hypothetical MCDA in the context of coral reef management. The potential interventions are shown in blue, and represent a subset of the interventions presented in Table 1.1. The example criteria, which, in this case correspond to biophysical outcomes, are listed in orange in the center, and are based on the recommended monitoring outcomes for coral reef resilience from Obura and Grimsditch (2009).

Predicted outcomes/criteria (such as coral diversity, herbivore biomass, disease) shown in orange can also differ for each intervention, and the specific mathematical relationship between criteria and interventions will differ and may not be linear. It is not necessary for all criteria to apply to all alternatives. In many cases, criteria will not be weighted equally depending on stakeholder preferences. This combination of changes in biophysical outcomes across interventions that are mapped to decision criteria, the differential weighting of criteria, and additional decision criteria that may not be captured by the biophysical models results in a complex decision-making landscape involving tradeoffs that benefits from a structured approach. Objective functions define the optimum values across criteria. For example, coral cover can always be maximized, while the optimum macroalgae value could be a threshold, and cost will likely always be minimized. Given all the inputs, criteria, and weights, the MCDA will generate a ranking of alternatives.

There are many different ways to structure the analysis, and the appropriate operational format will emerge out of the adaptive management process. For example, the decision about which intervention to utilize is far more nuanced than simply considering each intervention in isolation as represented in Figure 3.5. It is far more likely that there will be a series of interventions at different times and that these will be combined with management of local stressors. That said, in an iterative, adaptive management context, first evaluating each of these interventions by biophysical, economic, and social criteria using MCDA can lead to an understanding of relative differences across interventions that could be useful for subsequent analyses. For example, it may be revealed that, based on the understanding of their risks and benefits, certain interventions are either “dominant” (will always be preferred) or “dominated” (will never be preferred). The actual alternatives analysis will more likely be structured around particular scenarios, such as conventional stressor management in conjunction with differently timed intervention activities. Because there are many different ways to structure the problem, the site-specific context requires stakeholder and participatory modeling to establish objectives, goals, and criteria in an iterative way.

Evaluating sensitivity and uncertainty, as described for the biophysical models, informs tradeoff analyses as well. Depending on the specific software program that is used, it is often possible to evaluate cutoffs where one alternative is preferred over another, and how sensitive the ranking is to specific assumptions. For example, if coral cover is given a higher weight by stakeholders and decision makers as a key biophysical outcome, and the sensitivity analysis reveals that a small change in weighting of that outcome leads to a different ranking of interventions or alternatives, then that is useful information to have and will focus the communication and discussion of results across stakeholders.

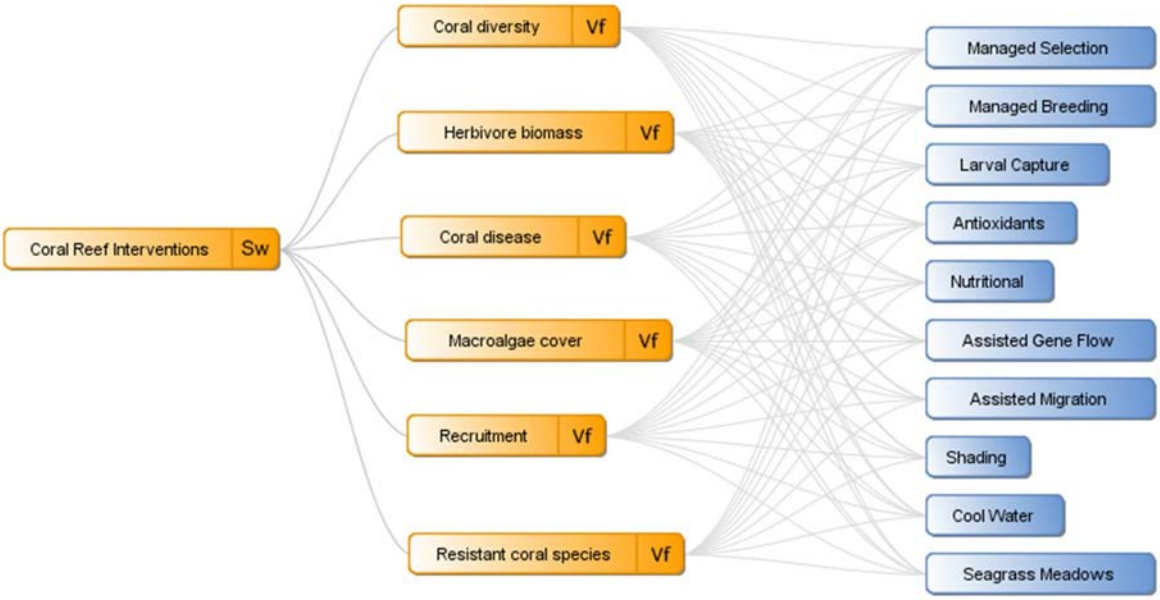


Figure 3.5 A hypothetical MCDA structure that relates possible coral interventions (blue) with coral management objectives (orange), linked by underlying biophysical models.

Example MCDA:

Brown et al. (2001) present an approach for protected area management at the Buccoo Reef Marine Park (BRMP) in Tobago that incorporates multiple objectives within a decision-making framework. The authors relied on MCDA and used the process to explore the impacts of four different development scenarios. The decision context was characterized by many different users in apparent conflict and by linkages and feedbacks between different aspects of the ecosystem and the economy. Diverse stakeholders were asked to weight different criteria, which were then incorporated into a tradeoff analysis to explore different management options.

Decision Trees

Decision trees represent another way to structure a decision. In this case, rather than evaluate tradeoffs across interventions on the basis of biophysical outcomes and criteria, a set of scenarios are developed and probabilities assigned to specific outcomes associated with each intervention. It is then possible to identify the optimal "path." Some decision trees are qualitative and can simply take the form of flow charts without assigned probabilities and are useful for structuring the decision context and developing conceptual models.

Example Decision Trees:

Flower et al. (2017) developed a general guide and decision tree for assisting coral reef managers in understanding the ecological implications of monitoring data that could inform a management response. They developed a guide for interpreting the temporal trends of 41 coral reef monitoring attributes as recorded and published by seven of the largest reef monitoring programs. As part of this guide, they proposed several decision trees to use in evaluating monitoring results. The tree is used to potentially distinguish across causal stressors given site-specific observations.

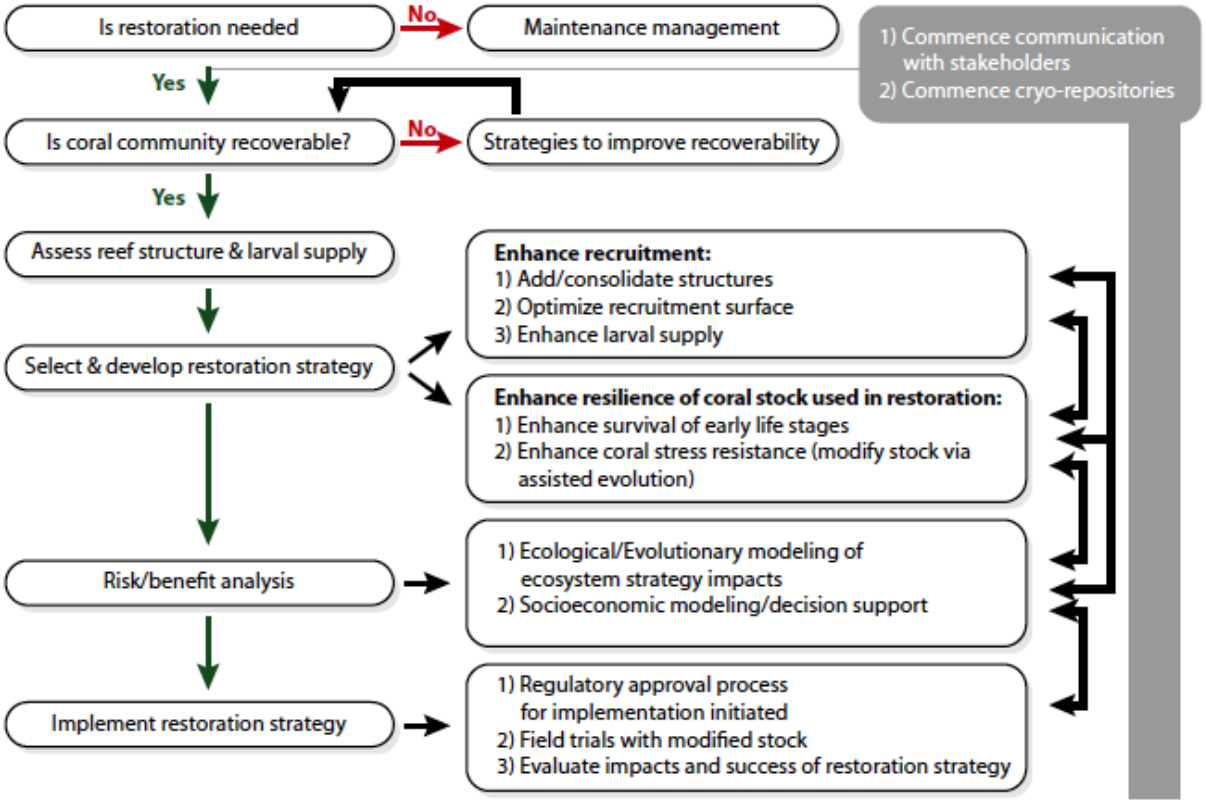


Figure 3.6 A qualitative decision tree for determining whether to implement coral interventions. SOURCE: van Oppen et al., 2017.

Van Oppen et al. (2017) proposed a decision tree for determining whether to incorporate assisted evolution (a term used for a variety of interventions) into restoration initiatives as part of a management strategy to enhance climate resilience of coral reefs (Figure 3.6). In this decision tree, a more structured decision methodology is nested under "Risk/benefit analysis," including ecological modeling of ecosystem strategy impacts (biophysical modeling as described in this document) and socioeconomic modeling/decision support.

System Dynamics Models

System dynamics models represent causal interactions within a system or population as hypothesized mathematical relationships that represent system behaviors and interactions over time. These models capture feedback structures that generate observed behaviors and effectively

integrate natural system dynamics with social constructs for policy analysis and decision making. These kinds of models often use "stocks and flows" to represent key parameters and their relationships. Stocks and flows, as a specific kind of system dynamics diagram, could represent healthy versus bleached populations, or healthy versus susceptible populations where different kinds of susceptibilities could be represented depending on the specific drivers present in the system.

Example System Dynamics Model:

Bartelet and Fletcher (2017) present a systems-based model developed to explore two different hypotheses about the spread of coral viruses in the Caribbean. They developed two simulation models based on the competing hypotheses about the origins and diffusion dynamics of a coral reef virus to make inferences about possible future behaviors. Figure 3.7 presents one version of the disease diffusion model based on a hypothesis that the virus originates from outside the coral colony (e.g., the result of the disposal of untreated human sewage in surrounding waters). It depicts a model diagram in terms of stocks and flows to quantify mechanisms surrounding a coral disease outbreak in the Caribbean. In this case, stocks (boxes) represent coral populations, and the flows (arrows) represent the relationship between different kinds of populations and infection and recovery rates. The four stocks in the model in Figure 3.7 include the susceptible coral population, the infectious coral population, the recovered coral population, and the white

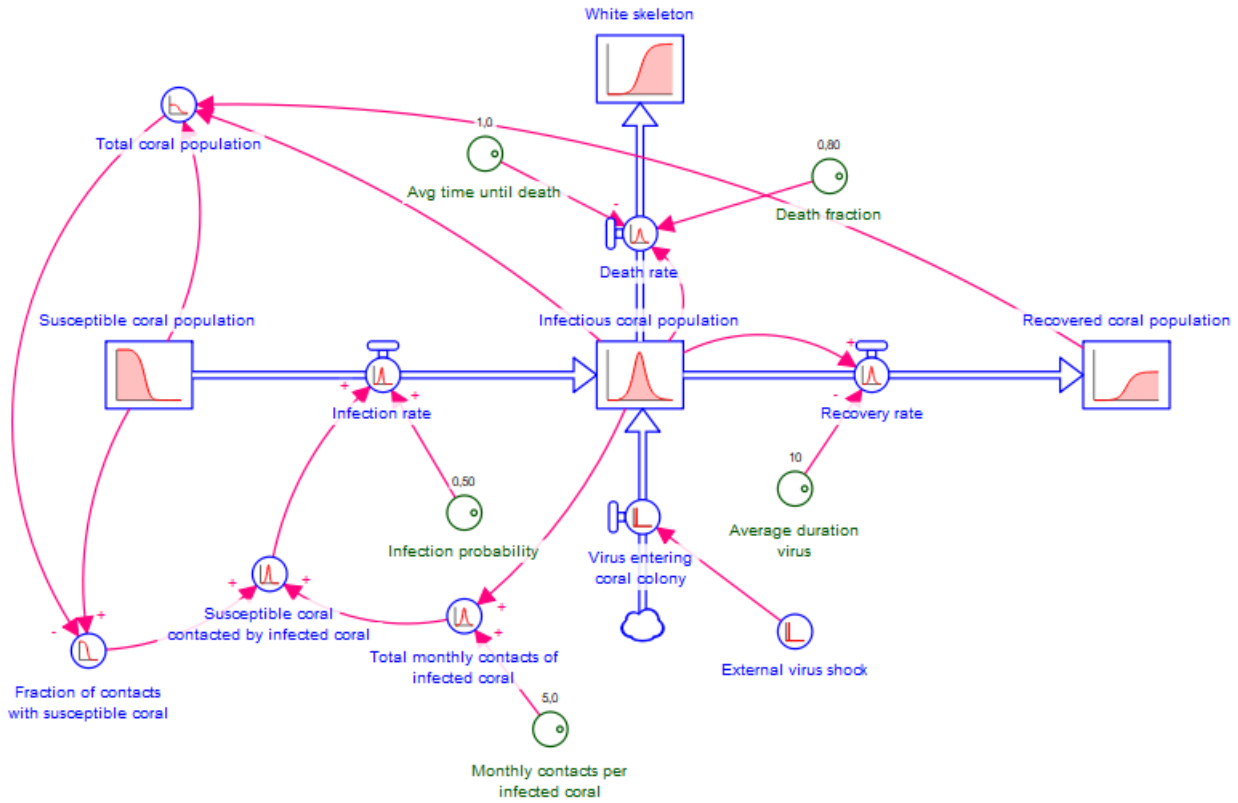


Figure 3.7 A system dynamics model of disease diffusion in a coral reef. Flows are represented by the blue arrows and stocks are the boxes. SOURCE: Bartelet and Fletcher, 2017.

skeleton population (e.g., where the live coral tissue has died). These models provide a structure upon which to prioritize research, test assumptions and hypotheses, and evaluate implications of policy and management decisions.

Bayesian Networks

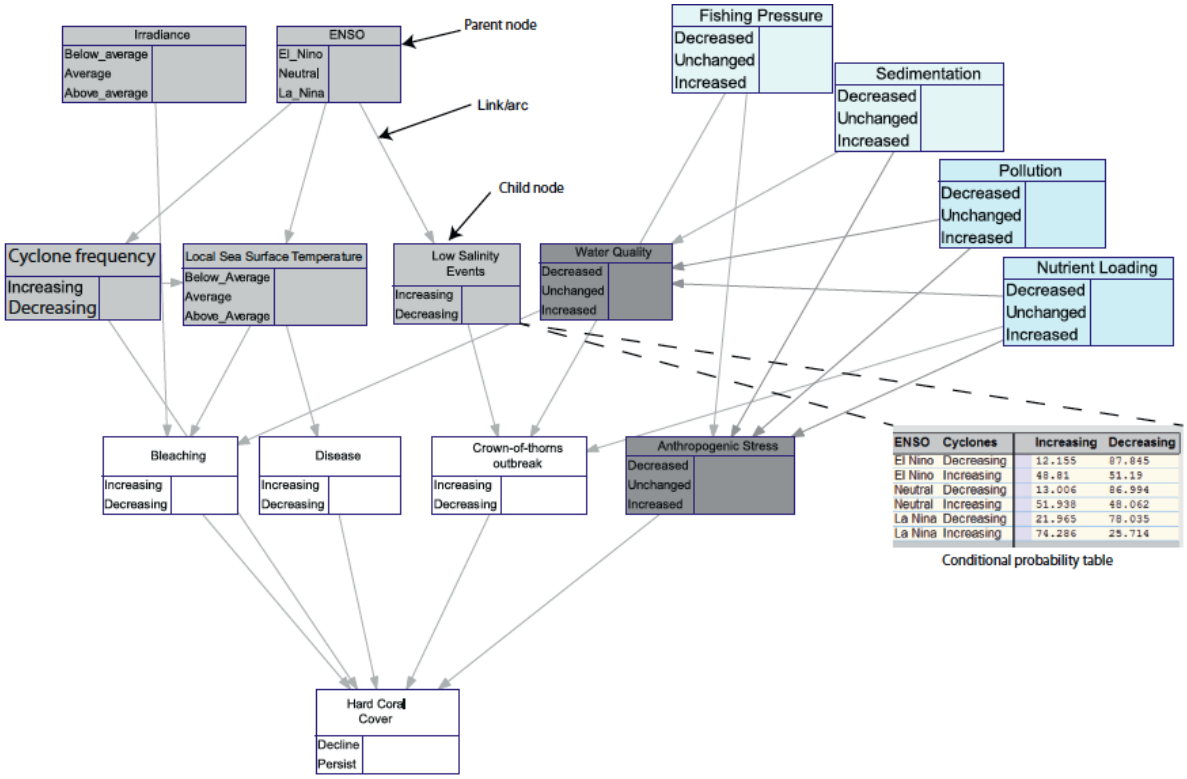
Bayesian networks offer another alternative for structuring decision making and will be the focus of a more complete example in Chapter 4. Key activities and hypothesized relationships are identified by nodes and connecting lines in a graphical format. These graphical models represent probabilistic and conditional dependencies among nodes, and frequently though not necessarily imply causation. The nodes in a Bayesian network define relationships and provide the ability to conduct inference on the relationships and dependencies across nodes. Bayesian networks are also known as Bayesian belief networks, the latter term used most prominently in cases where conditional probabilities in the network are informed by expert elicitation.

Bayesian network design may be based on a conceptual model for the specific application and can incorporate results from the underlying biophysical modeling to generate conditional probability tables to quantify the relationships across nodes. Environmental data or information on drivers and pressures can relate probabilistically to biological and ecological variables which in turn relate probabilistically to ecosystem values. Bayesian models are particularly useful for application in adaptive ecosystem management programs in which data may be limited, risks and benefits are poorly understood, and biophysical modeling inputs are poorly constrained and highly uncertain, but where there are opportunities for learning and adjustment (Chen and Pollino, 2012; Nicol and Chades, 2017; Nyberg et al., 2006) and potentially where expert opinion can complement data (Martin et al., 2005).

Example Bayesian Networks:

A number of examples of the use of Bayesian networks for coral management can be found in the literature. Carriger et al. (2019) demonstrate the process and utility of a Bayesian network for assessing delivery of ecosystem services in a hypothetical coral reef conservation situation. Franco et al. (2016) used coral reef carbonate balance (or rate of change) as the output node in construction of the Carbonate Budget BBN (CARBNET). The structure of the network was initially developed based on literature review, then modified based on expert consultation. It includes multiple levels of parent-child node relationships from the upstream climate change and anthropogenic disturbance nodes (e.g., coastal development, atmospheric carbon dioxide), to the associated pressures on ecosystems (e.g., sediment load, sea surface temperature), to the direct effects (e.g., turbidity, coral bleaching), to the presence of bioerosive (e.g., sea urchin) or bio-constructor taxa (e.g., coral carbonate production), and finally the calcium carbonate budget outcome. The relationships between nodes, as conditional probability tables, were parameterized based on a combination of original data collection and literature review, and then the relative influence of these evaluated with a sensitivity analysis. In another example, Ban et al. (2014) used a Bayesian network to structure their expert elicitation process to estimate the effects of the interaction of multiple stressors and related management options where data about the effects of these interactions were incomplete. Figure 3.8 provides an overview of this model, and the structure of Bayesian networks generally. The Capturing Coral Reef & Related Ecosystem

Services (CCRES) project has developed a publicly-available Bayesian network called ReefReact (https://ccres.net/resources/ccres-tool/reef-react) to predict the probability of coral reef cover for several selected years across different climate scenarios. The model, originally developed for Indonesian coral reefs, includes nodes for cyclone occurrence, disease outbreak, sediment exposure, grazing rate, and algal growth rate. Coral cover is predicted for several different years.



ENSO	Cyclones	Increasing	Decreasing
El Nino	Decreasing	12.155	87.845
El Nino	Increasing	48.81	51.19
Neutral	Decreasing	13.006	86.994
Neutral	Increasing	51.938	48.062
La Nina	Decreasing	21.965	78.035
La Nina	Increasing	74.286	25.714

Figure 3.8 A Bayesian network modeling relationships between coral reef metrics and stressors. Nodes shown in blue are drivers of synthesis nodes that change the microenvironment of coral reefs leading to adverse outcomes, shown in white. The dark grey nodes represent the combined effect of upstream nodes, including fishing pressure, sedimentation, pollution, and nutrient loading. Other pressures include cyclones, surface temperature, and salinity, leading to bleaching and potential disease. SOURCE: Ban et al., 2014.

Step 4: Select interventions or combination of management activities and determine evaluation metrics

The performance of different intervention strategies against objectives in the short and/or long term will inform strategy choice. Benefits (environmental, ecological, social, and potentially cultural), risks, costs, and tradeoffs should be reconsidered given the new quantitative information before a preferred strategy option is chosen. Once the intervention, set of interventions, or combination of management actions has been selected, it is important to establish a set of evaluation metrics for monitoring that link to the decision criteria developed based on management objectives. For example, a decision criterion might be to increase coral cover and diversity to create fish habitat (Hoey and Bellwood, 2011; Williams and Polunin, 2001). The associated evaluation metrics might then be abundance and diversity of coral and fish

species measured at appropriate time intervals. Measurable evaluation metrics that relate to the biophysical models will form the basis of the monitoring program discussed in in the next step. A variety of biological community, disturbance, ecological process, and site characteristic metrics have been proposed in the context of evaluating coral reef health and resilience (e.g., Ford et al., 2018; Lam et al., 2017; McClanahan et al., 2012; Obura and Grimsditch, 2009).

Molecular tools across the "omics" —including genomics, transcriptomics, proteomics and metabolomics—provide important metrics of intraspecific biodiversity, short-term responses to individual and suites of stressors, gene expression under changing conditions, and metabolic homeostasis. Genetic variation is a key component of resilience of populations, and determines the ability of organisms to respond to a variety of environmental parameters and stressors (Levin and Lubchenco, 2008). Proteins can mediate responses to stressors including elevated temperatures, reduced or elevated oxygen levels, and toxicant exposure. Metabolomics is the study of metabolite production, which is another indicator of an organism's state (Lohr et al., 2019; Quinn et al., 2016; Vohsen et al., 2019). Together, these molecular techniques can provide diagnostic tools that might be applied to evaluate the success and effectiveness of management actions and interventions. As such, they could be important tools for helping guide the allocation of limited financial, human, and institutional resources towards protecting corals and coral reefs.

In addition to the "omics," a number of physiological and ecological metrics provide insight into coral resilience. Physiological measures include growth rates, calcification, fecundity, productivity, constituent composition (e.g., lipids), algal symbiont density, and colony morphology (Edmunds and Gates, 2002; Putnam and Edmunds, 2011). Ecological attributes include survivorship, size-age distributions and coral population demographics, percent coral cover, coral diversity, rugosity, and recruitment patterns (Hughes and Connell, 1999). Survivorship, growth and recruitment in combination provide insight into fitness (Reusch, 2013), and hence the likelihood that coral species or populations can be sustained under environmental change and proposed intervention strategies. Beyond corals, associated ecosystem properties such as herbivore biomass and diversity can provide insight into ecosystem function and health (McClanahan et al., 2012). The physiological and molecular techniques are of particular value due to their ability to detect changes in real time, hours, days, and weeks versus many ecological indicators that are responsive over months, years, and decades (Aswani et al., 2015).

Steps 5 and 6: Implement interventions, and initiate and sustain a monitoring plan

Targeted monitoring is a critical component of an adaptive management plan in order to feed back to assessment and adjustment of management strategies. Monitoring provides data on predicted biophysical metrics, both to compare to model predictions over time and thereby improve the underlying biophysical modeling, but also to demonstrate and evaluate how well objectives are being achieved. Effective monitoring programs are based on the management objectives identified in Step 1 (Legg and Nagy, 2006), and the decision criteria and evaluation metrics identified in Step 4 based on these management objectives. Some of these monitoring targets, such as the "omics" and physiological metrics, can be monitored for change within short time scales. However, longer term monitoring is required to measure changes in community and ecosystem level metrics such as species diversity, persistence of key reef functional groups, and resilience (including longer term recovery) to disturbance (SER, 2004). There will be a

progression of metrics from near-term survival, to reproduction, to long-term persistence and resilience to monitor over time (Seddon, 1999).

Monitoring should also inform the identification of causes of strategy failure. Monitoring local stressors such as water quality or human activities could improve understanding of intervention outcomes as well as identify times where conventional management strategies would be reassessed. Monitoring the causes of failure would also involve monitoring for potential risks, such as the introduction of pathogens or nonnative species.

Steps 7, 8, and 9: Evaluate, communicate, and adapt

As interventions are applied and monitoring data comes in, the final three steps of the adaptive management circle involve evaluating progress toward decision objectives, communicating the results of the monitoring program, and potentially adapting or revising the management strategy. The monitoring data, especially when compared to model expectations, may reveal issues that were previously unknown, or may suggest localized dynamics not captured by the original decision model (e.g., the presence or absence of particular fish species and their relevance to coral health). If unintended consequences are observed, then the underlying biophysical modeling should be updated to reflect the evolving understanding of coral reef dynamics in the context of management activities. A passive adaptive management approach consists of trying one model or approach at a time. Compared to this, an active adaptive management approach, where multiple models or approaches are implemented in an experimental manner, enhances learning and the long-term outcome. Active adaptive management is more likely to be optimal compared to passive adaptive management under higher uncertainty, objectives that encapsulate higher risk tolerance, faster rates and broader applicability of learning, and lower costs of monitoring (McCarthy and Possingham, 2007).

A key aspect of the adaptive management approach is the ability to obtain initial data for intermediate outcomes in order to modify the management intervention accordingly. For example, a stated goal might be a 20% increase in coral cover over some period of time. There will be intermediate outcomes on the path to achieving this overall goal and a formalized process for monitoring improvement will help to inform the ongoing efficacy of management alternatives. These intermediate outcomes can be evaluated in different ways; one approach is formalized through “results chains,” a tool for helping teams clearly specify their theory of change behind the actions they are implementing (Margoluis et al., 2013).

CONCLUSION

Structured decision processes and tools exist that will help coral reef managers develop objectives and implement new and potentially risky intervention strategies. The chapter identifies a number of cases where these tools have been used to guide coral reef management. While they have largely been utilized in the context of managing local stressors, they are easily adapted to evaluating tradeoffs across other kinds of management interventions.

Conclusion: Although many tools exist for structured decision making to evaluate interventions as part of a reef management strategy, there is no single generalizable approach and no substitute for working through a structured decision process with stakeholders in the local context. This effort provides a data- and values-informed basis for selecting and evaluating management options against a set of objectives.

Recommendation: A structured adaptive management framework that considers all drivers and pressures affecting coral reefs should be developed to evaluate tradeoffs across alternatives and identify when and where new coral intervention(s) will be beneficial or necessary. This framework should include:

- **Engagement of a broad set of stakeholders to establish objectives and courses of action that reflect community values.**
- **Development of models tailored to the local environmental and ecological setting, management objectives, and preferred intervention options.**
- **Targeted monitoring of short- and long-term metrics of reef health and resilience.**
- **Iterative evaluation and adjustment of management strategies.**

4
Illustrative Model of Decision Tools

This chapter provides an example model and analysis for supporting decision making around coral intervention strategies. The committee's goal in providing this example is to illustrate the questions faced during the process of creating a modeling framework to inform decision making and the types of insights that can be gained. The committee uses a coral reef community model to simulate the effects of two example interventions on a simplified coral reef system: assisted gene flow and atmospheric shading. As part of this analysis, the committee illustrates the use of Bayesian networks to evaluate the impact of the interventions on management objectives in a probabilistic manner, represented by a range of model outcomes resulting from uncertainty around climate projections, intervention efficacy, and intervention risk. These efforts serve to exemplify the process described in Steps 2 and 3 in Chapter 3.

Because the committee's simplified model is for illustration only, the specific example results and analyses are not designed for adoption. The process of selecting management objectives and selecting interventions of interest begins with stakeholder engagement as described as Step 1 in Chapter 3. This is beyond the committee's purview because this involves extensive elicitation, consultation and deliberation and must be done with attention to the specific environmental, ecological, economic, and cultural contexts of an individual location (e.g. Gregory et al., 2012). Without the consideration of this social and local decision context, as well as detailed site-specific environmental data, the committee cannot use or develop any model to advise on the implementation of one or a combination of specific interventions. Additionally, evaluating all alternative interventions and their combinations for any real reef setting will be a computationally intensive effort (including more complex model structures to accurately represent each intervention) with many combinations of results to analyze. Instead, this illustration provides a concrete example of the construction of a decision support framework to analyze the risks and benefits of example interventions, evaluate the likelihood of achieving intervention goals under different scenarios, and communicate potential outcomes.

MODEL APPROACH

The committee constructed the simplest possible model that captures the coral reef dynamics relevant to two example interventions: assisted gene flow (the relocation of stress tolerant—in this example heat resistant—corals within their range) and atmospheric shading (in this case through marine cloud brightening or marine sky brightening). The committee's approach is to construct a general, "strategic" model appropriate for qualitative and comparative interpretation, as opposed to a realistic, "tactical" model appropriate for quantitatively precise predictions (May, 2001). As described in Step 2 in Chapter 3, any model used in a decision-making process would require (a) tailoring the model structure to the dynamics most important to the location and risks and benefits of the intervention(s) under consideration and (b) basing model parameters on the local system. In addition, a tactical model and approach would require model validation as described in Chapter 3, such as by ground-truthing model outputs against independent data (e.g.,

whether coral declines occur in observed bleaching events; Baskett et al., 2009). The committee did not undertake such validation here, but presents a more strategic approach for the purpose of illustration. The committee's model serves as a communication tool to illustrate how the problem of identifying and choosing among restoration and intervention options to build reef resilience under climate change could significantly benefit from the use of quantitative models to inform the decision-making process. Quantitative models and associated analyses can open the door for reef managers and policy makers to assess and compare benefits and risks of available intervention options, and thereby make more informed strategy choices under uncertainty.

Biophysical Model

The committee developed a model that follows the dynamics (change over time) of the proportion of area covered by two functional groups of coral—fast-growing corals (such as branching corals) C_F and slow-growing corals (such as foliose corals or massive corals) C_S—as well as by macroalgae M (Figure 4.1). These focal variables provide the simplest possible representation of the committee's chosen metric of intervention success: coral cover. The two broad categories of coral morphology represent extremes in the range of possible coral life history strategies and responses to thermal stress in a community (Loya et al., 2001; Darling et al., 2012); a diversity in response strategies to disturbance among community members (high stress-tolerance versus fast regrowth) can drive overall community resilience (Baskett et al., 2014). This representation assumes that many ecosystem services and values correlate positively with coral cover. The inclusion of two broad categories of morphological types can also provide initial insight into structural complexity that can be related to multiple reef functions (Graham and Nash, 2013). In addition, the focus on coral cover for simplicity ignores ecological dimensions such as differences in growth rate, survival, reproductive output, and stress tolerance of coral recruits as compared to established corals (and other such differentiation in demography by coral stage or size). Inclusion of macroalgal dynamics allows for exploration of how local management of nutrient inputs and/or herbivorous fish affects macroalgae cover, which is likely to affect intervention success due to the added dynamic of competition with corals.

The proportion of cover of each coral population changes over time as a result of a set of dynamics (growth, baseline mortality, and competition) that happen continuously throughout the year and a set of discrete events (bleaching and recruitment) that happen once per year during the summer. Mathematically, these two sets of dynamics are represented with a pulse-impulsive or semi-discrete model structure, following Baskett et al. (2014) and Fabina et al. (2015). Thus, this representation captures bleaching mortality separate from background processes. The focal stressor is sea surface warming driven by climate change; for simplicity of this illustration, additional possible global-change-dependent stressors such as ocean acidification (OA) and stronger storms are ignored.

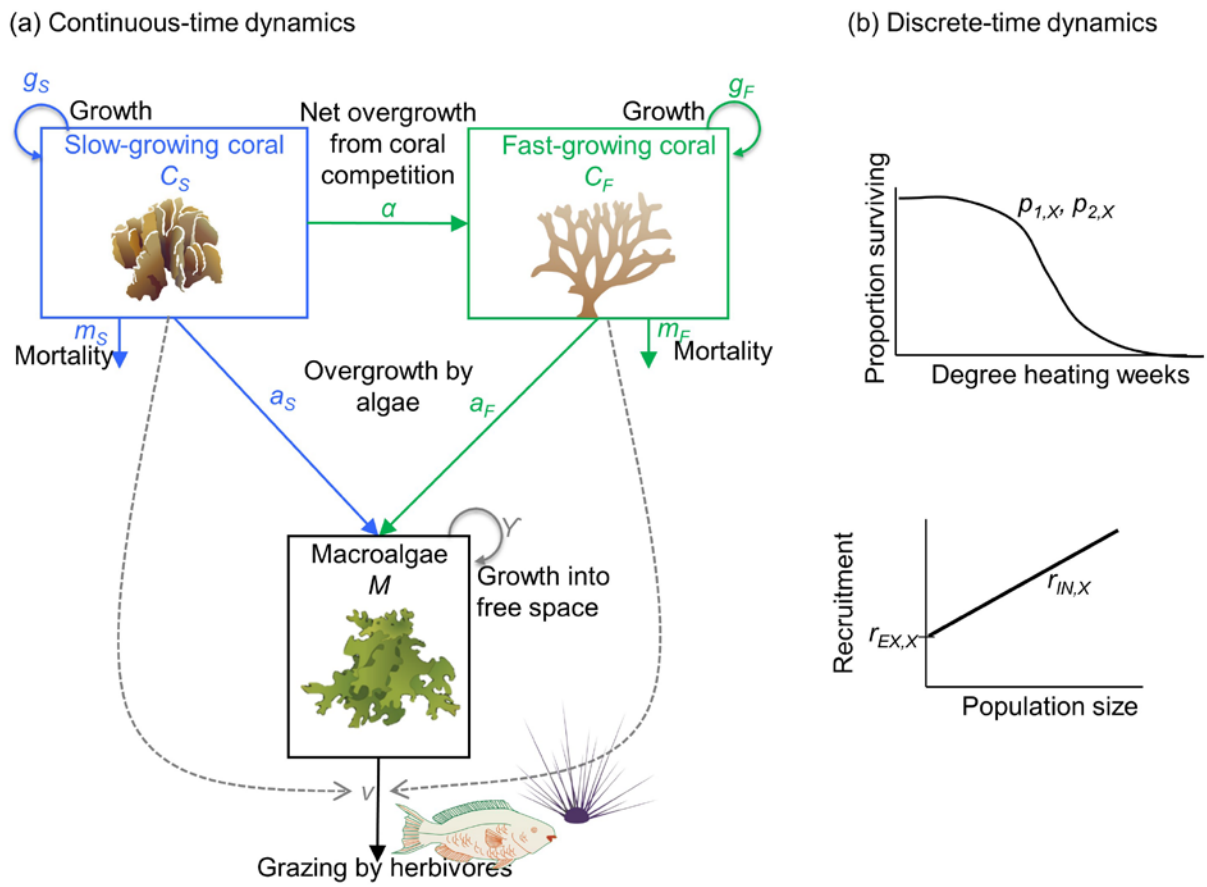


Figure 4.1. Conceptual diagram of the simple coral-macroalgae community model. (a) Continuous-time dynamics, where boxes identify the populations that change over time (slow-growing corals, fast-growing corals, and macroalgae) and arrows indicate processes determining continuous dynamics (competition, growth [lateral extension], and mortality) and their directionality of impact. Dashed lines indicate the influence of coral cover on grazing rate by herbivores. (b) Discrete-time dynamics, with survival from bleaching dependent on the amount of thermal stress (measured as degree-heating weeks) and both internal and external recruitment.

To model the continuous dynamics of growth, baseline mortality, and competition (Figure 4.1a), the committee built on a commonly-used framework by Mumby et al. (2007), which has been examined and extended for many studies (Anthony et al., 2011; Baskett et al., 2014; Blackwood et al., 2011, 2012; Fabina et al., 2015; Fung et al., 2010; McManus et al., 2018). Specifically, given the proportion of available habitat P (P=1 for a pristine habitat and P<1 with habitat destruction) each population grows into free space ($P- C_F–C_S–M$) at a rate g_X for each coral X (X=F, fast-growing, or S, slow-growing) and a rate γ for macroalgae. Growth captures somatic growth processes that extend the proportion of area covered. In addition, the model includes competition as net overgrowth by the superior competitor of each pairwise interaction, where the fast-growing coral overgrows the slow-growing coral at a rate α and macroalgae overgrows both corals at a coral-specific rate a_X. Herbivorous fish graze on macroalgae at a baseline rate v without corals, and the grazing rate increases with increasing coral cover. Each coral also

experiences background mortality at a rate m_X. Together, the mathematical representation of the continuous dynamics is:

Fast-growing overtop slow-growing

Coral baseline mortality

$$\frac{dC_F}{dt} = g_F C_F(P - C_F - C_S - M) - a_F M C_F + \alpha C_F C_S - m_F C_F \qquad \text{Eq. 1}$$

$$\frac{dC_S}{dt} = g_S C_S(P - C_F - C_S - M) - a_S M C_S - \alpha C_F C_S - m_S C_S \qquad \text{Eq. 2}$$

$$\frac{dM}{dt} = \gamma M(P - C_F - C_S - M) + M(a_F C_F + a_S C_S) - \frac{vM}{1 - (C_F + C_S)} \qquad \text{Eq. 3}$$

Growth into free space

Algal overgrowth of coral

Herbivore grazing, concentrated by increasing coral cover

To model the discrete dynamics (Figure 4.1b), each summer ($t = \tau$), both bleaching mortality and recruitment occur as discrete events. The proportion of mortality due to bleaching is modeled as a function of predicted degree heating weeks (DHW; see section on "Natural Adaptation" for DHW calculation). Annual bleaching-related mortality $\mu_X(\tau)$ is assumed to follow a Gompertz cumulative distribution function (Figure 4.2; Ricklefs and Scheuerlein, 2002) with coral-specific shape parameters $p_{1,X}$ and $p_{2,X}$. Specifically, $p_{1,X}$ mainly influences the amount of coral mortality at low DHW values and $p_{2,X}$ mainly skews the curve to the right towards higher DHW, representative of higher thermal tolerance (see Figure 4.2). Then the proportion surviving bleaching $h_X(\tau)$=1−$\mu_X(\tau)$ is

$$h_X(\tau) = \exp[-p_{1,X} \exp\left(p_{2,X}\, DHW(\tau) - 1\right)]. \qquad \text{Eq. 4}$$

After bleaching mortality, the total area available for new recruits at time τ is the total area of hard substrate available for coral and algal colonization (*P)* minus the remaining cover from each population:

$$L(\tau) = P - M(\tau) - h_B(\tau)C_B(\tau) - h_F(\tau)C_F(\tau). \qquad \text{Eq. 5}$$

Each coral population receives new recruits through internal recruitment at a per-capita amount (proportion cover added) $r_{IN,X}$ and external recruitment at an amount $r_{EX,X}$. The external recruitment can provide initial insight into the role of connectivity between locations, but the focus on a single location does not explicitly account for how variability in conditions and climate impacts across locations might affect recruitment, including recruitment declines that might arise from anthropogenic impacts such as pollution and sedimentation as well as coral regional declines (Richmond et al., 2018). In addition, macroalgae receive a small amount of internal recruitment $r_{IN,M}$ based on the amount of macroalgal cover as might occur from spores and external recruitment $r_{EX,M}$ as might occur from spores and drift algae. The inclusion of external recruitment can allow both coral and macroalgae recovery from zero cover. Therefore, the total area potentially covered by all recruits is

$$N(\tau) = r_{IN,S} h_S(\tau) C_S(\tau) + r_{EX,S} + r_{IN,F} h_F(\tau) C_F(\tau) + r_{EX,F} + r_{IN,M} M(\tau) + r_{EX,M}. \qquad \text{Eq. 6}$$

If the total area covered by recruits $N(\tau)$ exceeds the total area available $L(\tau)$, then recruitment fills the remaining area available, with the relative proportion of recruits for each coral group held constant.

The cover for each coral group after both bleaching and recruitment is then:

$$C_X(\tau^+) = h_X(\tau)C_X(\tau) + \frac{\min(L(\tau),N(\tau))}{N(\tau)}(r_{EX,X} + r_{IN,X}h_X(\tau)C_X(\tau)), \qquad \text{Eq. 7}$$

and the macroalgal cover after recruitment is:

$$M(\tau^+) = M(\tau) + \frac{\min(L(\tau),N(\tau))}{N(\tau)}(r_{IN,M}M(\tau) + r_{EX,M}). \qquad \text{Eq. 8}$$

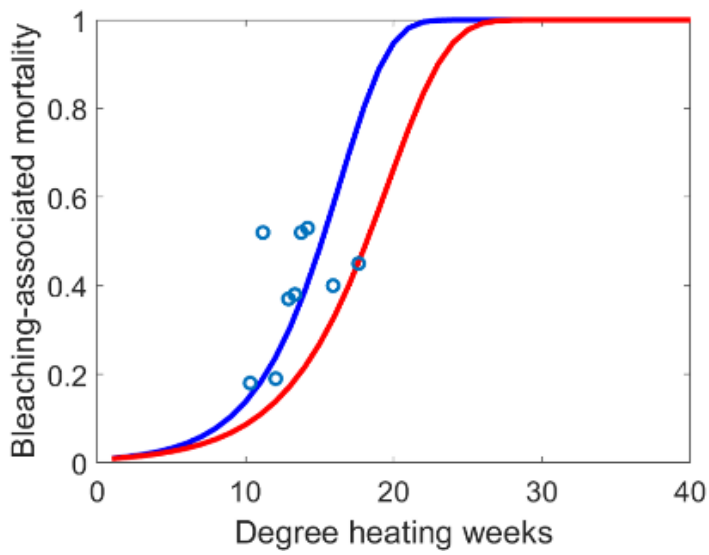


Figure 4.2 Bleaching mortality in response to cumulative warming (measured as degree heating weeks) during summer modeled as a Gompertz distribution function. The blue and red lines are examples used here for the fast-growing and slow-growing coral groups, respectively. Blue circles are mortality observations from the 2005 mass bleaching event in the Caribbean (Buddemeier, 2011). Slow-growing corals are assumed to be less thermally sensitive than the fast-growing corals (Loya et al., 2001), captured by the rightward skew of the bleaching mortality curve.

Natural Adaptation

The extent to which the rate of natural adaptive processes (whether through acclimatization, phenotypic plasticity, and/or genetic adaptation) by corals can keep up with the rate of global warming has been the focus of numerous studies in the past two decades (e.g., Baker, 2003; Barshis et al., 2013; Fitt et al., 2001; Hughes et al., 2003; Pandolfi et al., 2011; Pratchett et al., 2013). Projections of coral reef persistence into the future under climate change without adaptation typically predict coral collapse regardless of future climate scenario (i.e., under committed climate change), while those that account for adaptation predict that coral persistence depends on climate scenario and the level of adaptive diversity in the population (Donner, 2009;

Baskett et al., 2009; Logan et al., 2014; Bay et al., 2017). Specifically, adaptation at the intensities expected under typical population sizes and levels of natural selection often lead to coral persistence under more moderate but not more severe climate scenarios. In particular, the rate of climate change outpaces the rate of evolution under more severe scenarios (Baskett et al., 2009; Bay et al., 2017). Therefore, models that ignore the potential for natural adaptation bias their results towards the need for earlier and more significant intervention even under moderate climate scenario. Likewise, models without adaptation are likely to be biased against the value of moderate interventions in supporting coral cover. In addition to avoiding this bias, accounting for natural adaptation allows for a process to represent the benefit of interventions that accelerate adaptation, such as assisted gene flow.

In this model, the potential for natural adaptation is represented using "rolling" climatologies (Logan et al., 2014; Box 4.1). The typical approach to predict bleaching, such as that done by the NOAA Coral Reef Watch program, is to calculate the cumulative heat stress above the mean summertime maximum temperature on a given reef. For example, Coral Reef Watch first calculates the mean maximum monthly (MMM) annual temperature climatology in a given reef over a fixed period of time (1985-1993) and then sums thermal anomalies above that climatology (e.g., anomalies 1°C above the MMM) over a 12-week period to calculate Degree Heating Weeks (DHW). Different amounts of DHWs are then used to predict real-time bleaching and mortality. The DHW concept has also been applied to monthly sea surface temperature outputs from global climate models to predict future bleaching rates (e.g., Donner et al., 2005). In this case, a Degree Heating Month (DHM) calculation is used, and then converted to the DHW index using a conversion factor of 4.3 (weeks per month, Donner et al., 2005). To simulate the possibility that corals can adapt or acclimatize to more recently experienced changes in temperature, a climatology can also be calculated based upon a window that "rolls" in time relative to the recent past (e.g., Logan et al., 2014). For example, a model that uses the average temperature in 1970-2050 to calculate the anomaly in 2051 (i.e., the most recent 80-year window) would assume adaptation to more recent temperatures as compared to a model that uses 1920-2000. The time period over which the climatology is calculated can be shorter or longer in duration to represent faster or slower rates of adaptation, respectively (see Box 4.1 for an extended description of this calculation). For example, a model that compares 2051 temperatures to those experienced by corals from 2010-2050 (i.e., 40-year window) would result in fewer DHWs than if the average from 1970-2050 (80-year window) were used.

Projected Sea Surface Temperatures Forcing the Dynamic Coral Model

In the present modeling exercise, rolling climatologies calculated for reef cells located within the Caribbean region (157 reef cells; Figure 4.3) were used to calculate DHMs (converted to DHWs) based on bias-corrected global climate model data presented in Logan et al. (2014). Climate scenarios follow the representative concentration pathway scenarios (RCPs) developed by the Intergovernmental Panel on Climate Change (Collins et al., 2013). RCP 2.6 represents a strong mitigation scenario, and RCP 8.5 represents a "worst case" business as usual scenario. The RCP scenarios translate to predicted future climate trajectories based on global climate models and are incorporated into the average temperatures used in the DHW calculation. Specifically, for each

BOX 4.1
Calculating Thermal Stress Using Degree Heating Weeks

The typical approach to calculating Degree Heating Weeks from a time series of average monthly temperatures (Figure 4.1.1a, black lines) is to first calculate the maximum value for the average monthly temperatures (red dots, "annual monthly maxima") over a particular historic time window (shaded orange area), calculate the mean value (solid red line, "maximum of the monthly mean" climatology, or MMM, with a dashed orange line highlighting the value calculated within the window), and finally calculate the amount by which future temperatures exceed the mean monthly maximum each year (shaded yellow area, "Degree Heating Months"). The rolling window calculation for degree heating months continually shifts the time window (Figure 4.1.1b, blue shaded region) over which to calculate the MMM (blue dashed line as example calculation during one time frame for the MMM value indicated at the dark blue diamond, red solid line for shifting MMM over time) to phenomenologically represent adaptation to changing temperature over time. A narrower rolling window (Figure 4.1.1c, green shaded region) represents more rapid adaptation in the MMM due to adaptation to a higher average temperature. Therefore, the DHMs experienced are lower (Figure 4.1.1d), and bleaching mortality is lower (Figure 4.1.1e), under narrower rolling windows (green lines) compared to longer rolling windows (blue lines) and under rolling windows compared to a stationary window calculation (orange lines).

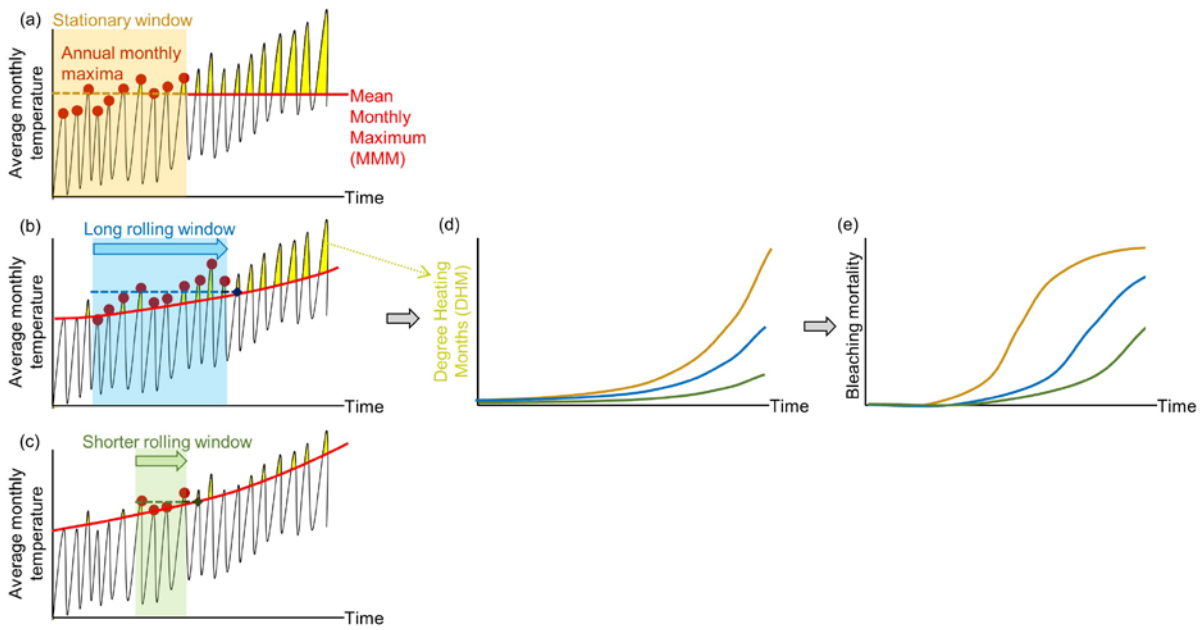


Figure 4.1.1 Illustration of the approach to calculate thermal stress experienced as degree heating months (which can be converted to degree heating weeks).

of the two climate change scenarios (RCP 2.6 and RCP 8.5), trajectories of DHWs for four different climatologies consisting of rolling windows of different length were produced (Logan et al., 2014; Figure 4.4). Because the trajectories in Figure 4.4 represent DHWs expected in bleaching years only, these are converted to DHW probability distributions for the Caribbean in any given year using observed DHW values bleaching and non-bleaching years during the past decade using Lough et al. (2018). In other words, Figure 4.4 was converted to DHW probability functions.

The outputs were then used as input into the bleaching survival function (Figure 4.2; Equation 4). A rolling window of 80 years was chosen as the default natural adaptation case because this window predicts high-frequency bleaching in severe but not more moderate climate scenarios (Logan et al., 2014), in line with mechanistic genetic models (Baskett et al., 2009; Bay et al., 2017). Then interventions that alter a coral's rate of adaptation are represented by alteration of the rolling window period, as described in the "Modeling the Interventions" section.

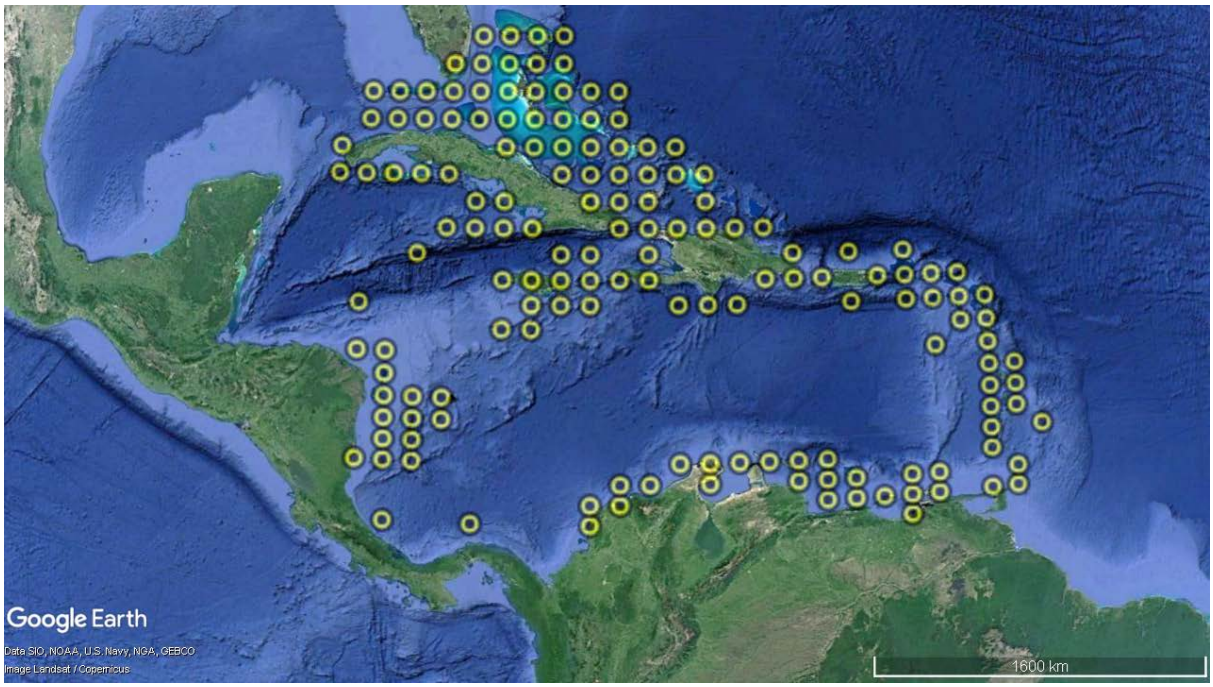


Figure 4.3 Depiction of the region and the reef cells for which rolling windows were produced. Latitudes range from 10.05 to 27.33°N, and longitudes range from 84.96 to 59.42°W. IMAGE SOURCE: Google; Data SIO, NOAA, U.S. Navy, NGA, GEBCO; Image Landsat/Copernicus.

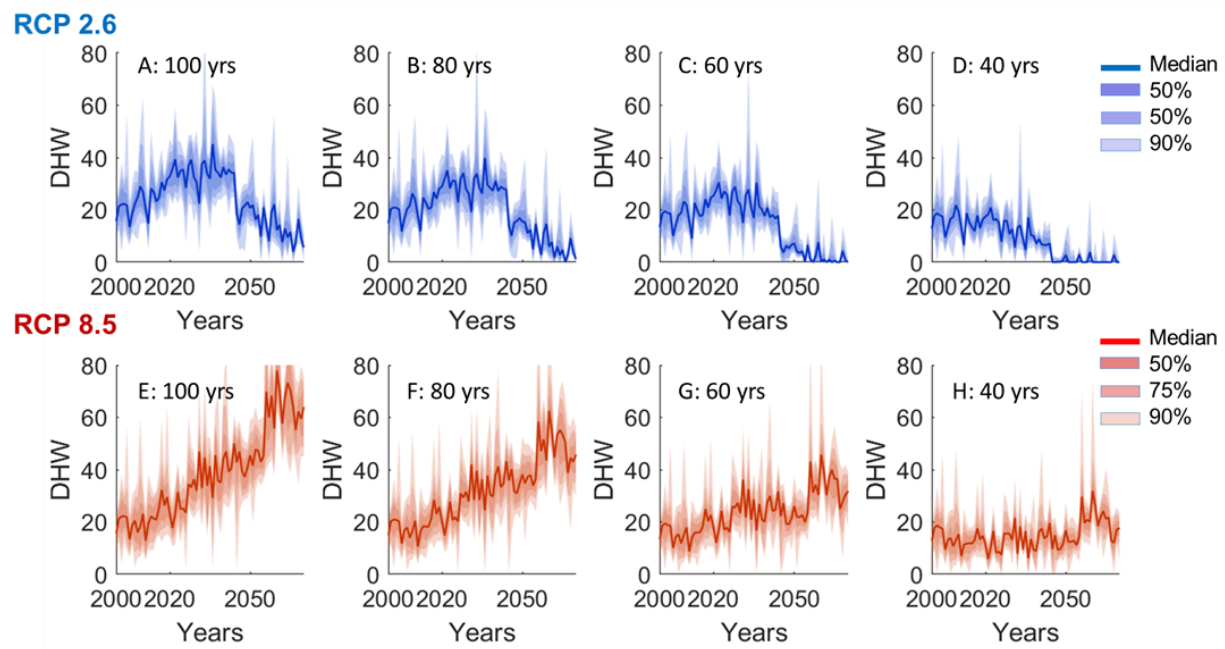


Figure 4.4 Projections of maximum expected degree heating weeks (DHW) for the 153 reef cells in the Caribbean generated using rolling climatologies with different window size: 100, 80, 60 and 40 years. DATA SOURCE: Logan et al., 2014.

Modeling the Interventions

Any modeling framework used in a decision-making process would need to clearly represent both anticipated benefits and anticipated risks of interventions. While broader decision-support frameworks should include environmental, social, economic, and cultural benefits and risks, in this example they are limited to ecological or biological only. Table 4.1 describes how biological and ecological risks and benefits are expected to occur based on the state of knowledge of each intervention (as described in the committee's first report; NASEM, 2019) might be assessed in the committee's model. The different modeling frameworks described in Table 3.2 (and the "Relevant mechanistic modeling framework" column of Table 4.1) can more mechanistically represent many of these risks and benefits for improved predictive ability. For example, while the rolling window calculation of DHWs implicitly accounts for genetic adaptation, explicitly accounting for genetic dynamics can allow the model to predict the expected evolutionary outcome from interventions that affect genetic composition rather than assuming a particular adaptive rate. These and other factors ignored here for simplicity (e.g., OA effects, coral size-dependent demography, additional coral species, spatially explicit dynamics associated with connectivity) would be an essential part of constructing a location-specific and intervention-specific model for an on-the-ground decision-making process.

As Table 4.1 illustrates, in some cases risks and benefits might affect the same value or process in the model, in which case mechanistic models are particularly necessary. For example, both risks and benefits of managed breeding arise through effects on genetic variance and fitness. Specifically, a key benefit of managed breeding is the potential to enhance genetic variance, and therefore adaptive capacity, through reducing the effects of drift and introducing novel genetic combinations. However, such enhanced genetic variance might pose a risk if it includes the

Table 4.1 Anticipated benefits and risks of interventions and the biophysical parameters for modeling using the committee's example model

	Relevant interventions	Potential effect in committee's model	Relevant mechanistic modeling framework
BENEFIT			
Increase thermal tolerance physiologically	Pre-exposure, algal symbiont manipulation, microbiome manipulation, antioxidants, and nutritional supplementation	Temporarily increase coral survival at a given DHW (lowering $p_{2,X}$ in $h_X(\tau)$)	Physiological model
Increase thermal tolerance via genetic adaptation	Managed selection, managed breeding, genetic manipulation, assisted gene flow	Narrow rolling window for calculating the DHW value in $h_X(\tau)$	Genetic model
Reduce exposure to thermal stress	Shading, mixing of cool water	Reduce DHW experienced	Oceanographic model
Reduce exposure to OA stress	Abiotic OA interventions, seagrass meadows and macroalgal beds	Incorporate OA-dependency for coral growth (g_X)	Structured population model
Increase disease tolerance	Antibiotics, phage therapy, microbiome manipulation	Decrease coral background mortality (m_X)	Disease dynamics model
Enhance population size	Managed breeding, gamete and larval capture and seeding, managed relocation	Increase in coral external recruitment ($r_{EX,X}$)	Structured population model and genetic model
RISK			
Reduced fitness (e.g. outbreeding depression, domestication)	Managed breeding	Increase coral background mortality (m_X)	Genetic model
Reduced rate of adaptation	Shading, mixing of cool water, abiotic OA interventions, seagrass meadows and macroalgal beds	Longer rolling window for DHW value in $h_X(\tau)$	Genetic model
Tradeoff between stress tolerance and other demographic processes	Managed selection, assisted gene flow, antioxidants, algal symbiont or microbiome manipulation, pre-exposure, OA interventions	Decrease coral growth (g_X) and/or increase coral background mortality (m_X)	Physiological model
Disease or other pest introduction	Managed relocation	Increased coral background mortality (m_X)	Disease dynamics model
Destabilization of beneficial versus deleterious microbes	Microbiome manipulation, antibiotics, phage therapy	Increased coral background mortality (m_X)	Physiological model
Increased macroalgal growth	Nutritional supplementation, macroalgal beds to reduce OA	Increase in algal growth (γ)	Community model with explicit herbivore dynamics

maintenance of maladapted genes that would otherwise be lost under natural selection. In addition, depending on the approach to managed breeding, there might be a risk of loss of genetic variance if the approach disproportionately favors a subset of genotypes ("sweepstakes events"; Crow and Denniston, 1988; Hedgecock, 1994; Lande and Barrowclough, 1987). A genetic model could capture how these potential risks and benefits combine to determine genetic variance and fitness and therefore the overall outcome. Analogously, both risks and benefits of antibiotics arise through effects on disease prevalence; in addition to potentially benefiting corals by reducing disease, antibiotics might destabilize beneficial microbes and promote resistance to antibiotics in deleterious microbes, and therefore a key risk is increased disease prevalence. A model that incorporates the dynamics of both beneficial and deleterious microbes with both antibiotic-susceptible and antibiotic-resistant types could mechanistically determine the balance of risk and benefit from different approaches to this intervention. While relevant mechanistic modeling frameworks are suggested in Table 4.1 based on the target process of a given intervention (e.g., genetics, physiology), in some cases a combination of frameworks will be necessary to capture the full array of risks and benefits, as discussed in Chapter 3.

For the purpose of this modeling study, two example interventions that impact different processes in the system have been chosen for illustration: assisted gene flow (for increased thermal tolerance) and atmospheric shading (for reduced exposure to thermal stress). Importantly, the model results are only an example of the potential benefits, risks, and limits of these interventions. The model ignores unanticipated risks or benefits, which could be analyzed through scenario planning (assessing a range of plausible future scenarios, usually qualitatively; Peterson et al., 2003). In addition, the model has only minimal accounting of the potential for ineffective intervention or intervention failure (whether due to scientific or human error), which can be analyzed by modeling a probability of failure (no benefit realized) or of partial benefit. The model includes the probability that shading may occasionally fail and thus the benefit potentially not achieved every year (described in more detail below). However, it does not include potential failure of assisted gene flow, such as the possibility that assisted gene flow might not increase adaptive capacity due to moving the wrong individuals to the wrong place or at the wrong time. Mechanistic models can account for uncertainty in whether anticipated benefits are realized.

Atmospheric shading interventions cool the sea surface over coral reefs either locally, regionally, or globally (Gattuso et al., 2018). In this example, local- to regional-scale atmospheric shading (e.g., as marine cloud brightening) is simulated as reductions in DHW exposure during the bleaching season using hypothetical estimates of shading efficacy. The benefits of shading are modeled simply as a lowering of DHW exposure during thermal anomalies using a low efficacy level of 0.3˚C cooling during summer. For simplicity and to focus on the primary anticipated benefit, the potential for shading to reduce macroalgal growth is ignored, an effect to consider in a more predictive model. The risk from shading is represented as reduced rates of adaptation and consequently enhanced heat stress in years of shading system failure, or potentially decommissioning. Specifically, when shading is implemented, the rolling window for calculating DHW values is increased by 20 years. In addition, the likelihood of atmospheric shading failure (and therefore corals experiencing baseline rather than shading-adjusted DHW) is drawn from a Poisson distribution with mean $\boldsymbol{\lambda}_{SF}$=0.1. While there are other potential risks to atmospheric shading, such as changes in local precipitation and ocean

productivity or deposition of aerosols (salts) on neighboring land, these are not included in the model.

Assisted gene flow (a type of managed relocation) is the active transport of genes within a locally-adapted population to other locations within their range where they are expected to match future climate conditions (Aitken and Whitlock, 2013). Because the model represents a single focal location, assisted gene flow (applied to both coral types) is modeled as the introduction of corals with high thermal tolerance genes from locations that have historically experienced, and therefore are adapted to, high thermal stress. This is represented in the model as narrower rolling windows for calculating the mean climatology that determines the DHWs experienced (60 or 40 years as two levels of intervention, potentially determined by how distant of a location from which to select transported corals). The approach of shifting rolling windows (as opposed to shifting the parameters in the bleaching mortality function in equation 4) was chosen to bound the expectations for how much assisted gene flow might increase stress tolerance based on a representation of an adaptive process. The addition of the transported coral fragments or recruits with assisted gene flow also adds a small amount to coral cover, which is added to the coral recruitment $r_{EX,X}$ (10% increase in value) for each focal coral X.

Risks of assisted gene flow include disruption of local adaptation to non-climatic factors and other sources of outbreeding depression, accidental transport of invasive pests and pathogens, and tradeoffs between enhanced thermal tolerance and additional demographic processes (e.g., growth, physiological maintenance, and resistance to additional stressors that underlie survival). A typical risk involved for assisted gene flow is outbreeding depression for hybrids between the native and transplanted corals (Aitken and Whitlock, 2013). Accidental introduction of invasive species is typically invoked for assisted migration outside a species' range (Hewitt et al., 2011) rather than assisted gene flow over small distances. However, in coral systems, accidental introduction of diseases might pose a significant risk for assisted gene flow due to the large geographic range for many coral species (basin-wide in some cases) and prevalence of diseases, with regional heterogeneity in incidence, that significantly affect coral cover (Rosenberg et al., 2007; Ruiz-Moreno et al., 2012), hence its inclusion here. These risks are modeled as a decrease in growth g_X and an increase in baseline mortality m_X for each translocated coral type X. Both of these changes can represent effects of outbreeding depression and tradeoffs between stress tolerance and other demographic processes, and the change to baseline mortality can also represent the effects of accidentally introduced diseases. Changes in growth and mortality are increased with increasing intervention levels under the assumption that achieving a greater increase in thermal tolerance might involve transport from more distant or environmentally different locations and therefore incur greater risk. For each 20-year window of accelerated adaptation, the value for growth decreases by 10% and the mean amount by which mortality increases is 0.05 yr^{-1}. In each simulation, an increase in mortality is drawn from an exponential distribution given the intervention-dependent mean to represent stochasticity in the likelihood of pest or pathogen introduction and uncertainty in the amount of demographic tradeoffs. This approach of adjusting baseline mortality represents the potential for non-local pathogens as endemic (permanently present) rather than epidemic (short-term outbreak) diseases.

No intervention (i.e., maintaining all parameters at default values) is modeled as a counterfactual. Establishing a counterfactual provides an essential comparison point in a decision

framework for understanding the potential for the focal interventions to enhance the likelihood of coral reef persistence and sustained delivery associated with the ecosystem services. In the context of rapid climate change, the counterfactual can provide insight into the damage prevention afforded by an intervention strategy, and the value of early action.

Conventional management of local stressors is considered across all scenarios (no intervention, shading, assisted gene flow) by exploring a range of values for herbivory rate (v) and macroalgal growth rate (γ; Table 4.2). These two distinct parameters and processes interact to determine the overall macroalgal dynamics (net growth). These parameters can represent how local management and reef context might affect the likelihood of intervention importance and success. Increasing herbivory rate provides initial insight into the effect of sustainable fisheries management. Decreasing macroalgal growth provides initial insight into the potential effect of nutrient control. As with the two sample interventions, this exploration is a subset of possible actions and outcomes from conventional management, which could also include actions to reduce local anthropogenic impacts on coral growth, survival, and recruitment (e.g., from sedimentation and pollution). The herbivory and macroalgal growth rate values are set at model initialization, to represent the local conventional management context, while the parameter changes associated with atmospheric shading or assisted gene flow change in a specified "deployment year," to represent additional interventions implemented in the local context. Interventions (or intervention effects) occur continuously after the deployment year until the end of the simulations. As with the coral interventions, these explorations represent illustrations of how one might develop and analyze a decision framework for the interaction between local management controls and interventions; predictive frameworks for these local management controls would also rely on more mechanistic models (e.g., explicit herbivore dynamics for herbivorous fish control).

Numerical Analysis

The expected outcome were analyzed for different intervention scenarios by simulating equations 1-8 in MATLAB. The MATLAB code was developed by two committee members, and verified by a third. The code and output are available in the NASEM public access file on request. Initial proportional coral cover was randomly chosen to either represent potentially initially degraded (5%) or "pristine" (30%) coral conditions. The model is initially simulated with non-intervention default parameter values until an intervention time point (deployment year), then parameter values are altered as described in the "Modeling the Interventions" section to implement interventions until the end of the simulated management horizon (2060). Within each one-year time step, (1) the discrete-time bleaching mortality and recruitment are applied according to equations 4-8 and (2) the continuous-time dynamics in equations 1-3 are numerically integrate over one year using the MATLAB function ode45.

In setting parameter estimates, ranges from the literature were used to the extent possible. For most of the parameters that describe the continuous-time processes of growth, competition, and baseline mortality, values are drawn from the ranges in Fung et al. (2010). Baseline mortality is informed by Madin et al. (2014), converted from discrete-time proportion mortality $p_{m,X}$ to continuous-time mortality rate m_X as $m_X = -\ln(1-p_{m,X})$. For bleaching mortality, parameters $p_{1,X}$ and $p_{2,X}$ of the Gompertz function are estimated by anchoring the mid-section of the curve in the

2005 Caribbean mass bleaching event (Figure 4.2). It should be noted that without calibration of the bleaching mortality parameters to a more extensive data in the region, outputs are associated with high uncertainty. A summary of parameter estimates for different interventions are presented in Table 4.2.

The vital rates of coral growth, recruitment, and mortality will inevitably vary between species and locations. Further, responses to new interventions are in many cases uncertain because the research and development necessary to establish how the environment or the ecosystem responds to intervention has not been carried out. However, because the purpose of this example is to provide an illustration of assessing the scope that new interventions might have in improving coral condition or preventing coral loss, the focus is on relative impacts rather than projecting absolute reef states that depends on precise parameter estimates.

Strategy design and simulations

The performance of the example interventions is assessed using a structured design that compares interventions individually and in combination. The combinations are referred to as "strategies" that constitute options (alternatives) for decision-making. For the purpose of this example all possible combinations of interventions and conditions at multiple levels were analyzed (Table 4.3), for a total of 192 strategy combinations. In reality, a subset of strategies can be identified where, for example, water quality and herbivore management are an agreed prerequisite for new interventions. Strategy-generation tables elicited with the help of reef managers and stakeholders can help narrow in on such a subset of strategy alternatives (Howard, 1988; Ohlson and Serveiss, 2007). Comparing all intervention combinations and all conditions, however, enables one to understand the extent to which interventions in strategies might synergize or antagonize (combined effect greater or less than the sum of each alone, respectively), and under what conditions. From the perspective of coral resilience, supporting multiple processes that together alleviate pressures, underpin survival, and promote growth and recruitment will increase the likelihood that the system can gravitate to a coral-dominated state (Anthony et al., 2015).

The design for intervention strategies (all combinations) is replicated for a set of conditions, specifically: early versus late deployment years, low versus high start states for coral cover, and moderate to severe climate change scenarios (Table 4.3). Exploring these combinations allowed us to examine under what condition(s) interventions have high versus low efficacy, and with what risks. For example, while early deployment of assisted gene flow may seek to stem coral decline, the associated risk of also introducing a pathogen may counter that benefit, especially for a high start state representing a healthy reef. Such examples are explored in the context of climate outlooks, intervention benefits, and risks to inform the discussion around decisions to deploy versus delay (Iacona et al., 2017).

Each line in the resulting design table hence provides the command structure for the 192 combinations in the model simulations. In this analysis, 10 simulations (trajectories) were run for each line in the design table (for a total of 1,920 simulations) using a Monte Carlo approach. The modeling was limited to only 10 simulations because the only source of stochastic variation was the temperature inputs, resulting in narrow confidence bands around coral and macroalgal

Table 4.2 Summary of symbols, functions, and default parameter values used in the model.

Symbol	Unit	Interpretation	Range	Source
C_F	Prop	Area covered by fast-growing corals	0 – 1	-
C_S	Prop	Area covered by slow-growing corals	0 – 1	-
M	Prop	Area covered by macroalgae	0 – 1	-
P	Prop	Proportion habitat available	1	-
g_F	yr^{-1}	Growth rate of fast-growing corals	0.5	Fung et al. (2010), Anthony et al. (2011)
g_S	yr^{-1}	Growth rate of slow-growing corals	0.3	Fung et al. (2010)
γ	yr^{-1}	Growth rate of macroalgae	0.8	Fung et al. (2010)
a_F	yr^{-1}	Rate of macroalgae over-growing fast-growing corals	0.05	Fung et al. (2010)
a_S	yr^{-1}	Rate of macroalgae over-growing slow-growing corals	0.07	Fung et al. (2010)
α	yr^{-1}	Rate of fast-growing coral over-growing slow-growing corals	0.03	Tanner et al. (1994)
m_F	yr^{-1}	Base rate mortality for fast-growing corals	0.1	Madin et al. (2014)
m_S	yr^{-1}	Base rate mortality for slow-growing corals	0.05	Madin et al. (2014)
v	yr^{-1}	Baseline grazing rate on macroalgae	0.4	Fung et al. (2010)
$r_{EX,F}$	Prop	External recruitment of fast-growing corals	0.001	Fung et al. (2010)
$r_{EX,S}$	Prop	External recruitment of slow-growing corals	0.001	Fung et al. (2010)
$r_{EX,M}$	Prop	External recruitment of macroalgae	0.001	This study
$r_{IN,F}$	nd	Internal recruitment of fast-growing corals	0.005	Fung et al. (2010)
$r_{N,S}$	nd	Internal recruitment of slow-growing corals	0.005	Fung et al. (2010)
$r_{IN,M}$	nd	Internal recruitment of macroalgae	0.005	This study
$p_{1,F}$	nd	Shape parameter 1 for fast-growing corals	0.02	This study
$p_{2,F}$	nd	Shape parameter 2 for fast-growing corals	0.28	This study
$p_{1,S}$	nd	Shape parameter 1 for slow-growing corals	0.02	This study
$p_{2,S}$	nd	Shape parameter 2 for slow-growing corals	0.23	This study
DHW	°C wk	Degree Heating Weeks		Logan et al. (2014)

NOTE: The term 'nd' indicates non-dimensional (relative) units.

projections. The probability of a thermal anomaly and its severity (as DHW) is drawn annually from a random distribution under predicted max DHWs from rolling windows. Intervention uncertainty and varying conditions were represented by the low versus high parameter estimates set to bracket their likely range (the "Levels" identified in Table 4.3). Ideally, a larger number of simulations should be run, that number being a tradeoff between precision and computing power available when modeling complex systems. This is especially so if the stochastic variation or

uncertainty of many different environmental and ecological model parameters are also included in simulations.

Table 4.3. Summary of conditions and interventions at increasing levels of intensity used in model simulations as part of the strategy design.

	Levels
Conditions	
Climate change scenario	RCP 2.6, RCP 8.5
Start state (total coral cover)	5%, 30%
Deployment year	2025, 2035
Interventions	
Algal growth (stimulated by nutrient load)	0.6, 0.2
Algal grazing rate (herbivores)	0.2, 0.6
Assisted gene flow (as rolling-window climatologies)	80, 60, 40 years,
Atmospheric shading (for 12 weeks during bleaching season, with risk of failure)	Nil, 6 DHW

NOTE: Model results were reported for years 2020, 2030, 2040, 2050, and 2060.

Results of Analysis

The focal output metrics for each of the 1,920 simulations is coral cover over time combined for the two coral groups. Figure 4.5 illustrates a selection of example trajectories from the model with varying levels of RCPs, conventional management, and assisted gene flow. Under RCP 2.6, low grazing and high nutrients (driving algal growth) and low start state (initial coral cover), coral cover is projected to decline further, while macroalgae cover is projected to increase. This trajectory occurs with and without assisted gene flow ("AGF" in Figure 4.5a,b). However, setting conventional management to high (high grazing and low nutrients; "BPM" for "best practices management") changes the outlook dramatically, but more so with conventional management alone than when high levels of assisted gene flow are introduced (Figure 4.5c vs. Figure 4.5d). This is explained by the risks associated with high assisted gene flow, with uncertainty in mortality effects manifested in Figure 4.5d as a broader confidence band around the trajectory line (the mean estimate). Under RCP 8.5, the situation is the same for the no/low conventional management scenario (low grazing and high nutrients), again with or without assisted gene flow (Figure 4.5e,f). While moving from low to best-practice conventional management does not improve the coral outlook by itself (Figure 4.5g), setting assisted gene flow to high in combination with high levels of conventional management leads to coral recovery and sustained cover to 2080 under RCP 8.5 (Figure 4.5h). These sample modeling results and the conclusions drawn from them are sensitive to the assumptions made around how different environmental, biological, and ecological processes interact and the strength of these interactions.

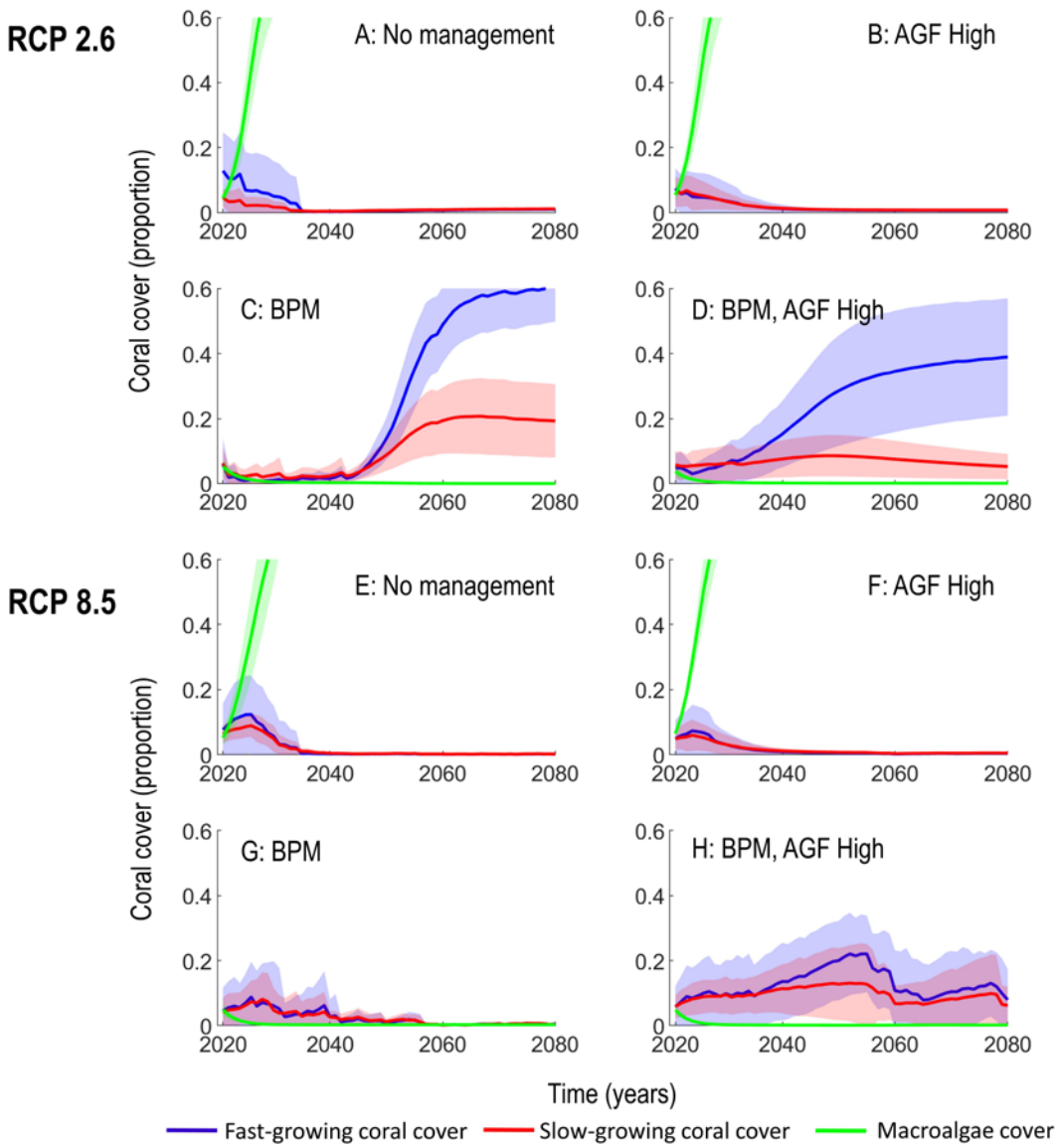


Figure 4.5 Example trajectories of coral and macroalgal cover under combinations of strong mitigation (RCP 2.6) and business-as-usual climate change (RCP 8.5), low versus high ("best practices") management (BPM), and low versus high rates of assisted gene flow (AGF). Blue, red and green trajectories and confidence bands (1 SD) are the fast-growing coral, slow-growing coral, and macroalgae, respectively. Each panel indicates a different management strategy based on select combinations of conditions listed in Table 4.3.

BAYESIAN NETWORK ANALYSES

The large number of model outputs (coral cover over time based on 192 combinations of conditions and interventions) produced by the model means that general conclusions cannot be drawn easily from inspecting the many trajectories of outcomes for corals and macroalgae. To identify which strategy solutions perform better requires the ability to query all dimensions of the results and evaluate their tradeoffs using one of the systematic approaches described in Step 3 in

Chapter 3. In this section, the committee uses a method whereby trajectories of dynamic and uncertain coral cover are converted to a network of conditional (Bayesian) likelihoods. The method is adapted from one described by Nicol and Chades (2017) but uses model outputs to replace expert opinion (see also Ni, 2011). Networks of conditional likelihoods have the advantage of translating easily to the language of risk (i.e., probability and consequence). While some uncertainty is accounted for in the outputs (mainly DHW), a fuller account of uncertainty will require that multiple sources of variation and uncertainty are hard-wired into the modeling. This will require a larger number of simulations to filter signal from noise. While results of the Bayesian network model (as well as the dynamic, mathematical mode) are presented non-spatially, it can also be presented spatially where geographic information systems (GIS) data are available and used as inputs (Gonzalez-Redin et al., 2016).

The method for converting the biophysical model output into data for a Bayesian network is described in detail in Appendix B. Ten data points of coral cover were collected at decadal time steps (2020 to 2060) and organized according to the scenarios identified in Table 4.3. In the current example, these ten points comprised all data points produced by the dynamic model. If more points were produced by the model (e.g., 1000 simulations per combination of interventions and conditions), an appropriate subset of those results can be sampled and exported to the Bayesian analysis. The data are then imported into Netica (www.norsys.com) using the method described by Ni et al. (2011) to populate an empty Bayesian network diagram that mirrors the data column headers.

Results of Analyses

In the following examples analyses, a basic exploration of the results of the modeling outputs of the dynamic coral reef model illustrates how one might use the output in a decision-making process for a set of example management questions. The results are analyzed using a Bayesian network to capture all model outputs as likelihoods, and then results brought together for comparison in a strategy (or consequence) table to inform decision-making. In a Bayesian network analysis, one or more parameters (each represented by “nodes”) are fixed at a chosen value in order to evaluate the relative impact the remaining parameters have on achieving those chosen states. Managers can translate their objectives into these fixed parameters. The following examples explore how selecting fixed coral cover as a simple objective, under selected timeframe and climate scenario conditions, influences the relative importance of other parameters, such as the need for intervention or improved management of local stressors.

Example 1: What will be required to sustain coral cover under substantial greenhouse gas mitigation (RCP 2.6)?

To address this question the Bayesian network is examined in diagnostics mode by locking in the objective of at least 20% coral cover as the dependent variable (0.2 to 1 range in node *CoralCover*) and the condition for RCP 2.6 (node *Scenario*). At the modeled endpoint of 2060, RCP 2.6 would represent average atmospheric temperature increases of about 1.5°C relative to preindustrial level, as compared to increases of about 2.7°C under RCP 8.5 (Collins et al., 2013). Note that 20% coral cover represents a relatively unambitious objective compared to more “pristine” historical state. High coral cover is now set as the primary management objective

(with 100% likelihood as the ambitious target). This setting updates the nine independent parent nodes.

In the illustrative results (Figure 4.6a), the distributions of likelihoods within each of the independent nodes provide indication of the node states or levels that contribute most to achieving high coral cover under RCP 2.6. For example, among all years in the modeled horizon, the coral cover objective has the highest likelihood of being met in years 2020 and 2060 (node *Years*). While this is at first counterintuitive, the result is consistent with the declining pattern of DHWs in Figure 4.6 for the rolling windows. In other words, as global temperatures start to stabilize mid-century under RCP 2.6, and surviving corals adapt, coral cover is expected to recover. Also, a high start state (coral cover in year 2020, in node *StartState*) provides the highest chance of meeting the objective of sustained coral cover. Further, a high grazing rate by herbivores on macroalgae (*Grazing*) improves the chance of achieving high coral cover. Therefore, under the particular parameterization and model structure used in this example, an example message would be that the management of herbivores are generally more important than new interventions (*AGF* and *Shading*) under RCP 2.6.

Example 2: What will be required to sustain coral cover under business-as-usual greenhouse gas emissions (RCP 8.5)?

To address this question, RCP 8.5 is selected in *Scenario* instead of RCP 2.6. The example results in Figure 4.6b illustrate three possible conclusions for this model structure and parameterization. First, the likelihood of sustaining coral cover declines precipitously with time (node *Years*). Specifically, there is a 4-fold greater chance of sustaining greater than 20% coral cover in 2020 compared to 2060. Second, the opportunity for a high assisted gene flow (*AGF*) effort to contribute to coral cover is increased compared to RCP 2.6. Third, the role of grazing remains significant. Given that the legacy of start state is likely to decline over time, it is assumed that the importance of high start state in the results is linked predominantly to years 2030 and 2040. Shading has a minimal role because its positive effects (nominally 6 DHW cooling) are offset by the shift to a longer rolling climatology window (due to slower rates of adaptation) in combination with the risk of shading failure. Cases such as this where a conclusion is a direct outcome of model assumptions illustrate how model explorations can identify crucial assumptions that require validation with data and exploration with more mechanistic models.

Example 3: What will be required to sustain corals on the long time horizon under business-as-usual greenhouse gas emissions?

To model the specific conservation goal of sustaining high coral cover in the long term under the business-as-usual climate change scenario, the target year is set to 2060 (node *Year*) under the RCP 8.5. Note that modeling of longer time horizons, to at least 2100, would likely be preferred as a representation of “sustained” coral cover, although uncertainty in climate predictions will increase for longer projections.

Under this illustration, an example central conclusion is that achieving high coral cover is now nearly three times as likely to occur under a high effort to support assisted gene flow (*AGF*; Figure 4.6c). Interestingly however, absence of shading (“Nil”) produces a higher likelihood of

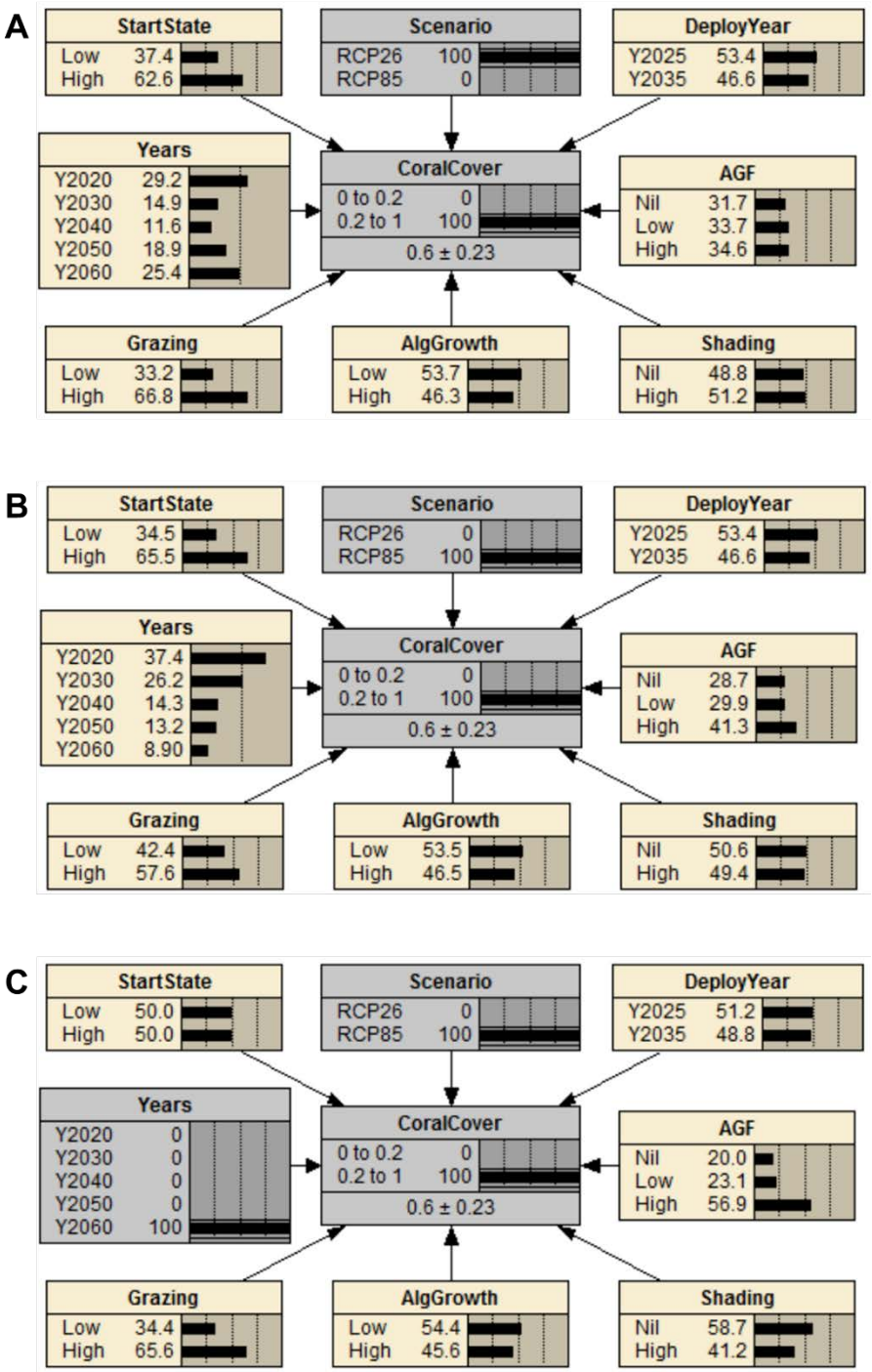


Figure 4.6 High-level summary result of the Bayesian network, integrating and synthesizing all outputs of the dynamic coral reef model. Results show distributions of conditional probabilities of global and local conditions and interventions needed to achieve the objective of achieving coral cover greater than 20%. See Table 4.2 for details of variables. Grey boxes indicate dependent (locked-in) objectives set by a decision-maker and yellow boxes indicate independent (non-pre-determined) nodes. Each panel (A, B, C) indicates a different set of locked-in objectives.

sustaining coral cover. The explanation for this is likely similar to that described under example 2: the 6 DHW cooling is offset by the shift to a longer rolling window for adaptation built into the model. Importantly, similar to the general RCP 2.6 scenario (example 1), there is twice the chance of sustaining high coral cover under severe climate change by 2060 under a high compared to low rate of algal grazing, a component of conventional management. The relatively low impact of high versus low algal growth compared to grazing is likely to be the result of the relatively low and narrow range of algal growth rates used in the model (0.2 yr^{-1} to 0.6 yr^{-1}).

Comparing management options

The three questions above are examples of diagnosing the system for the purpose of understanding what conditions and interventions most strongly drive high coral cover and when. While the examples show how one might inform decision making, they do not directly assess which interventions may produce the highest (or lowest) chances of success (i.e., meeting the primary objective). Such an assessment can be conducted by using the Bayesian network in predictive mode. In this case, the likelihoods of high coral cover (over 20%) are recorded while systematically varying conditions and interventions from Table 4.3 (Options A through E described below). The output of this analysis becomes a consequence table, which can be used to identify high-performing strategy options or alternatives (Gregory et al., 2012; Groves and Game, 2016). It is important to note that coral cover is only one example of an ecological objective, and that a more complete structured decision analysis will need to take account of additional objectives, including economic, social, and ideally cultural value sets (Gregory et al., 2012; Keeney and Raiffa, 1993).

Results are compared for two management horizons, year 2040 and 2060. The near horizon exemplifies how early assessment affects the expected detectability of intervention efficacy, whereas the longer horizon provides insight into whether interventions have longer-term potential as impacts of climate change (or mitigation) progress. Within these horizons are eight scenario combinations: RCP 2.6 vs. RCP 8.5, low vs. high start state, and early vs. late deployment year (2025 vs 2035, which can indicate the role of early versus late intervention in a race against time; e.g. Anthony et al., 2017) for new interventions (assisted gene flow and shading). Because RCP 2.6 and RCP 8.5 do not diverge strongly until after 2040 or 2050, comparisons of intervention performance between RCP 2.6 and RCP 8.5 at the year 2040 horizon provides limited information.

For the baseline option (**Option A** in Figure 4.7), grazing rate is set to low and algal growth to high, representing the current condition of many reefs. Furthermore, shading and assisted gene flow (AGF) are set to nil. High, or best practices, conventional management of local stressors (*BPM*) is included in the strategy options (**Option B**) by setting algal grazing to high and algal growth rate to low. **Option C** represents a strategy that deploys a high rate of assisted gene flow in combination with best-practice conventional management. This is achieved by selecting the 40-year rolling climatology (*AGF High*), which will include a downside risk of increased chance of disease mortality. **Option D** expands Option C by adding shading, specifically by simulating 6 DHW cooling during summer in addition to high rates of assisted gene flow and best-practice management. Lastly, **Option E** is a high rate of assisted gene flow and shading, but with a low level of conventional management. This option enables assessment of how important effective

conventional management is in combination with new interventions. The likelihoods that each strategy option (A to E) sustains coral cover above 20%, given the varying conditions, are illustrated in Figure 4.7.

Example insights that one might gain from this type of analysis are:

First, **Options C and D** (best practices management with assisted gene flow, and then with shading added) appear to be the only robust solutions that can sustain coral cover above 20% under either climate change scenario in this analysis. In the short term (year 2040), the analysis shows between 25% and 83% chance that Option C can achieve the objective (>20% coral cover), with generally higher likelihoods for early deployment (year 2025) for the interventions. In the longer term (year 2060), performance likelihoods are projected to be between 58% and 83% under RCP 2.6, and between 42% and 58% under RCP 8.5. For Option D, the most intensive strategy, performance likelihoods range between 17% and 58% in the short term. In the long term, this strategy performs better than Option C under RCP 2.6, and worse under RCP 8.5. As shading is the only factor separating Options C and D, these results suggest that net benefits of shading in the long term under RCP 2.6, become net risks in the long term under RCP 8.5 (potentially due to reduced adaptation). The particular predictions here suggest that Option C would be a more robust option than Option D. This outcome will inevitably vary with parameterization of the amount by which shading dampens and assisted gene flow accelerates thermal tolerance adaptation, and the likelihood of shading failure. Therefore, the illustration highlights the need to explore and resolve this potential antagonistic interaction with a more mechanistic model, such as a genetic model where the evolutionary outcome emerges from the thermal stress rather than assuming an adaptive rate.

Second, **Option B** (best practices conventional management only) performs better on its own (92% likelihoods of meeting the objective) than Option C (best practices conventional management and high assisted gene flow; 58% to 83%) in the long term (2060) under RCP 2.6. Under RCP 8.5, this reverses: Option C (42% to 58%) outperforms Option B (8%). In other words, in this analysis, risks of assisted gene flow (caused by disease mortality) outweigh benefits under the high-mitigation climate scenario, while the benefits of assisted gene flow outweigh risks for business-as-usual climate change.

Third, removing best practices conventional management (i.e., water quality and fisheries management) from Option D to produce **Option E** reduces its performance likelihoods to nearly that of the low management option with no interventions (**Option A**). This illustration highlights how two key conclusions could be based on this particular parameterization and analysis. First, conventional management on its own would very likely not be enough to sustain coral condition. Second, while new intervention strategies have scope to build critical coral resilience under business-as-usual climate change, their success requires sustained or intensified conventional management.

Year	Scenario	StartState	DeployYear	A: No management	B: Best-Practice Management (BPM)	C: BPM + High AGF	D: BPM + AGF + Shading	E: AGF + Shading
2040	RCP 2.6	Low	2025	8	12	29	30	8
2040	RCP 2.6	High	2025	8	17	50	42	13
2040	RCP 8.5	Low	2025	8	21	36	33	8
2040	RCP 8.5	High	2025	8	13	59	38	8
2060	RCP 2.6	Low	2025	8	92	58	83	8
2060	RCP 2.6	Low	2035	8	92	83	75	8
2060	RCP 2.6	High	2025	8	92	67	75	8
2060	RCP 2.6	High	2035	8	92	83	83	8
2060	RCP 8.5	Low	2025	8	8	42	17	8
2060	RCP 8.5	Low	2035	8	8	58	42	8
2060	RCP 8.5	High	2025	8	8	50	25	8
2060	RCP 8.5	High	2035	8	8	58	17	8

Figure 4.7 Results of the example Bayesian network analysis, identifying percent likelihoods (red to green scaled boxes) that a management strategy (options A to E) sustains coral cover above 20% over a variety of conditions (blue boxes). A: No intervention or change in management. B: Best practice management includes local stressor and fishing pressure control. C: Assisted gene flow (AGF) is added to best practices. D: Reef shading is added to "C." E: Reef shading and assisted gene flow are used without management of local stressors.

Importantly, all likelihoods presented in these analyses, including likelihoods for the low conventional management option, are associated with uncertainty. They are partly driven by the parameter values set for the different variables in the model (Table 4.2), including range boundaries set for interventions and other conditions (Table 4.3). This example illustrates how a Bayesian network analysis can identify particularly influential parameters, such as those related to conventional management (grazing rate and algal growth), that would require careful measurement for accurate predictions. In addition to context-dependent model formulation and parameterization, ground-truthing of model projections would be necessary to inform analyses that can guide strategy comparisons and inform decision analyses with confidence.

ADDITIONAL DIRECTIONS

Four general principles drive interest in modeling interventions to evaluate expected outcomes: (1) interventions could make a difference in sustaining coral cover over decadal timescales but incur uncertain risks; (2) some interventions may work better in certain conditions than others; (3) some interventions may work more or less effectively when they are implemented together; and (4) the order in which multiple interventions are implemented at a site may influence their success. As illustrated in this chapter, a structured decision-making framework informed by both a dynamic reef system model and a Bayesian network analysis can help managers identify and

quantify (with uncertainty) which interventions, or sequence of interventions, might best deliver management objectives. For example, the results from the particular model structure and parameterization used in this example would suggest that (1) assisted gene flow and shading can alter expected coral trajectories over decadal time scales, but risks can outweigh benefits under high mitigation scenarios; (2) these interventions are more likely to be effective with strong fishery management and nutrient control; and (3) assisted gene flow and shading are less effective together than separately given that the assumed risk of shading (slowed evolution) counteracts the benefit of assisted gene flow (accelerated evolution). While these results will certainly change with more mechanistic model and ground-truthed parameterization, these example conclusions illustrate how building and parameterizing a model for a target location and set of interventions can lead to insights that inform the local decision process of what, when, and where to intervene.

Additional analyses of this type of framework can inform other aspects of the decision-making process outlined in Chapter 3. For example, projections from this type of modeling framework can inform monitoring and adaptive management decisions such as what metrics might best indicate success and risks (starting from the array of possibilities in Table 4.1), when to expect detectable changes in those metrics and therefore when to evaluate success or risk (e.g., when trajectories diverge between the plots with different interventions in Figure 4.5), and what magnitude of outcomes in those metrics to expect (see Kaplan et al. (in press) for an example of this type of analysis). Comparing such expectations to observed outcomes leads to improved knowledge. In the adaptive management process, this knowledge is used to update the relevant modeling framework and thus inform improved management decisions (Holling, 1978; Walters, 1986; Walters and Holling, 1990).

A crucial component of any model analysis will be a sensitivity analysis. By quantifying the effect of uncertainty on the model outcome, parameter sensitivity analysis can indicate which empirical data might most improve model projections (Cariboni et al., 2007). Different parameters can also represent different environmental, ecological, or management contexts such that sensitivity analysis to such parameters can indicate where interventions might be most effective or risky (as illustrated by exploration of the different values of herbivory rate and macroalgal growth rate here). Functional sensitivity analysis can help identify the simplest possible model relevant to a set of interventions.

In addition to varying model inputs, different types of model outputs and analyses can inform decisions as they might depend on stakeholder and manager risk tolerance. For example, a model output and analysis focused on minimizing the likelihood of a risk, such as minimizing the probability of particularly low reef state, might be more relevant to a risk-averse manager. Another type of model analysis can be an evaluation of how benefits and risks depend on the decision process for when and where to intervene (including how long to intervene; the example model assumed continual intervention, or intervention effect, after the deployment year). Context-dependent or condition-dependent decisions might include whether to intervene before a forecasted bleaching event or after an observed bleaching event, or more generally, whether to intervene on healthier reefs or following coral decline, and how to stagger multiple interventions. In other words, a modeling framework of the type illustrated here can quantitatively evaluate

many of the intuitively-expected context dependencies for prioritizing intervention described in Chapter 2.

Conclusion: A successful modeling framework requires substantial effort in tailoring model structure and parameters to the decision context, risks, and benefits of the interventions under consideration, and local environmental conditions and reef ecosystem dynamics. As demonstrated by the committee's illustrative effort, the utility and payoff of this approach is the ability to identify

- **The conditions necessary for new and potentially risky interventions to outperform the no-action alternative under different future climate scenarios.**
- **The interventions expected to be most effective at achieving management objectives.**
- **Potential synergistic and antagonistic interactions across multiple interventions, including management of local stressors.**
- **The key dynamics and parameters to resolve empirically in order to improve the capacity to predict intervention efficacy and risks.**

Further applications of such modeling frameworks include identifying indicators for context- or condition-dependent decisions, monitoring, and adaptive management. The insight provided by a quantitative model enables decision makers and reef stakeholders to compare the benefits and risks of different intervention options with more clarity and transparency than provided by qualitative or conceptual approaches or by expert opinion only. The benefits of a quantitative model are greatest where local ecosystem and evolutionary dynamics are known, and when primary sources of uncertainty are considered.

5
Research Needs

Despite the rapid pace of research on coral biology and conservation that is occurring on a global scale, there are many gaps and unresolved issues that need to be addressed in the short and long term. The committee's review of the state of science in their first report (NASEM, 2019) illuminated many information gaps regarding the risks, benefits, and feasibility of the coral interventions. It is important to improve understanding of the potential interventions to inform their implementation. The best practices described in Chapter 3 and the description of the model in Chapter 4 identify priority areas where knowledge needs to be improved to create a detailed, reef-specific decision support tool. Generally, these include improved ways to identify, measure, and monitor fitness parameters of corals; greater understanding of factors that contribute to stress tolerance and associated tradeoffs for corals; and measuring the impact of interventions on demographic processes within reef ecosystems. With improved understanding, models can better predict outcomes of various reef management approaches. The committee divided research needs supporting this work into four broad categories (summarized in Box 5.1): (1) research on fundamental coral reef biology, (2) site-specific research relevant to a proposed intervention, (3) research to inform specific interventions, and (4) research to improve risk assessment and decision models. The committee ends this section by emphasizing the structural needs relevant to supporting community-based research efforts.

The decision process itself is a tool for identifying and prioritizing research needs. Articulation by stakeholders of preferred objectives and management options may narrow the scope of research needs by clarifying the relevant modeling approaches and the most pertinent reef dynamics to resolve. Structured decision analyses can also be applied to the design of research and development strategies with the objective of delivering interventions that can more effectively support reef persistence and resilience under climate change. This can start, for example, with the identification of management strategies (using strategy-generation tables, e.g., Howard, 1988) and their ties to the research needs in Box 5.1.

BOX 5.1
Summary of Research Needs

Research on fundamental coral reef biology

1. Identify the cellular mechanisms of bleaching, and how these pathways are influenced by recent thermal history, host genetics, symbiont type, and microbiome.
2. Identify underlying causes of coral diseases, and develop biomarkers of coral health, heat susceptibility, and disease diagnosis as well as ecosystem health.
3. Determine functional roles of and tradeoffs among, members of coral reef communities at multiple ecological scales from coral-associated symbionts and microbiomes up to the composition of coral species in reef communities.
4. Identify population structure, determine evidence for local adaptation, and define relevant management units for population recovery.

5. Develop methods to improve recruitment and survivorship for corals that are released, planted, relocated, or settled on reefs at the reef scale.
6. Develop extensive, freely available databases on coral communities, hosts, symbionts, and microbiomes to support studies on genotype-phenotype relationships, population structure, and community dynamics.
7. Identify species-specific threshold responses of corals to changes in temperature, light incidence, and ocean pH, as well as reef-scale threshold responses to disturbance and environmental change.

Site-specific research and assessment to help determine whether intervention is needed or possible

8. Identify local stressors that influence population recovery and determine whether stressors are likely to influence the success of interventions.
9. Develop appropriate metrics and recovery goals that assess the effects of the intervention on ongoing tolerance, health, fitness, and recruitment within the target management unit as well as on connected reefs.
10. Evaluate whether population recovery at a specific site can be achieved through translocation or managed breeding and if so, which intervention is most appropriate for recovery.
11. Identify host, symbiont, and microbial populations at candidate restoration sites, to ensure treatments or manipulations aimed at improving coral physiological performance can achieve recovery goals.
12. Assess in a site-specific manner the benefits, risks, and chances of success for implementing environmental interventions.
13. Identify the most appropriate site-specific, synergistic management and intervention strategies that together provide greater chance of success and reduced risks than the sum of the impacts of each intervention alone.

Research to improve assessment of the benefits, efficacy, and risks of specific interventions

14. Develop protocols for control of pathogens (biosecurity and quarantine).
15. Develop effective approaches to modify symbiotic algal and/or microbiome populations.
16. Develop effective approaches to determine whether corals that are released, planted, relocated, or settled on reefs contribute to recovery goals, while reducing risk to ongoing adaptation and ecological processes.
17. Develop and test genome-editing methods in a wide variety of ecologically important coral species.
18. Develop methods of delivery for nutrients, probiotics, antibiotics, phage therapy, and antioxidants at reef scales.
19. Assess feasibility, potential benefits, costs, limitations, and risks associated with environmental interventions.

Research to inform risk assessments and modeling

20. Targeted monitoring to evaluate performance, improve benefits, and minimize or manage risks.

21. Iterative model design to reduce uncertainties and improve model predictions to increase confidence in the decision support framework.

RESEARCH ON FUNDAMENTAL CORAL REEF BIOLOGY

Coral reefs are intensively studied ecosystems and much progress has been made in understanding coral ecosystem dynamics through monitoring of key reef species (see overviews in Wilkinson, 2008; Jackson et al., 2014). A focus on discovery and applied science to improve the understanding, management, and resilience of individual coral reefs, as well as the broad ecosystem, will continue (Lam et al., 2017). However, effective restoration approaches for reefs require an improved understanding of what factors underpin coral health and how these lead to reef scale resilience. Though these topics are inherently broad, there are a number of research areas that can be prioritized to aid the decision analysis and implementation of current and future restoration approaches identified in the committee's work.

1. Identify the cellular mechanisms of bleaching, and how these pathways are influenced by recent thermal history, host genetics, symbiont type, and microbiome.

The processes that lead to expulsion of the endosymbiotic algae (Symbiodiniaceae) partner that result in the characteristic signs of bleaching are still poorly resolved at the cellular level. The current state of knowledge of these cellular mechanisms was comprehensively discussed in the first committee report (NASEM, 2019). Active ejection of the symbionts from coral cells is likely, combined with impairment of symbiont photosynthesis (Downs et al., 2002; Weis, 2008; Baird et al., 2009). Definitive identification of the cellular mechanism of how bleaching occurs is critical to assessing the thresholds of bleaching across different species. This information is also central to refining the modeling parameters for heat stress sensitivity of corals and evaluating potential mitigation outcomes provided by intervention strategies. The cellular triggers of coral bleaching can be influenced by historic exposures, and intervention strategies such as pre-exposure rely on low-level heat stress to increase resilience to later high temperature exposures. Defining how the host genotype, algal symbionts, and even the associated microbiome interact to trigger bleaching across both historic and current temperature thresholds is key to minimizing uncertainty associated with most interventions.

2. Identify underlying causes of coral diseases, and develop biomarkers of coral health, heat susceptibility, and disease diagnosis as well as ecosystem health.

Some measure of coral health both before and after an intervention is implemented is required to evaluate the need for, and impact of the intervention. The underlying molecular, cellular, and physiological processes that facilitate a healthy functioning coral remain poorly resolved due to the complex interplay between the host, its algal symbionts (Symbiodiniaceae), and other microbial partners. Biomarkers (attributes and substances indicative of a biological state/condition) are critical tools in biomedical research and clinical practice for assessing the health status of patients. However, in corals there are currently no universally accepted biomarkers for healthy or stressed individuals, and homeostatic baselines are also generally unavailable. Multiple studies have used a range of approaches to link cellular physiological

functions to stress and, ultimately, the health of individual corals including growth (Edinger et al., 2000), fecundity (Linton and Warner, 2003), productivity (Scheufen, et al., 2017), calcification (Anthony et al., 2008; De'ath et al., 2009), protein assays (Downs et al., 2000), lipid and fatty acid constituents (Bachok et al., 2006), gene expression (Louis et al., 2017) and metabolite chemistry (Farag et al., 2018; Sogin et al., 2016) among others. However, the cellular response of coral holobionts to stress is still unclear because it is complex and driven by numerous pathways that interconnect and are likely different among coral species. Furthermore, biomarkers or even simple physiological tests for differences in heat or disease resistance are generally lacking or just being developed. Morikawa and Palumbi (2019) tested known biomarkers, environmental sensing, heat mapping, and physiological profiling as predictors of tolerance to bleaching in nursery corals. Muller et al. (2018) measured heat tolerance and disease tolerance along with their associated tradeoffs among clones of one Caribbean coral species. But further work and refinement across species is clearly needed.

In addition, teasing apart the biomarkers associated with the coral host and the algal partner can be challenging because understanding of biomarkers of stress for the symbiont lags behind that of the host. Continued efforts to identify and develop easy-to-use biomarkers and physiological assessment of coral health and stress resistance for species targeted in restoration efforts is a priority area that can aid restoration approaches into the future. Rapidly advancing technologies in the areas of “omics,” nanotechnologies, sensor development, and imaging are being applied to corals and will no doubt aid and accelerate filling this knowledge gap.

Disease and increased incidence of disease(s) in a coral population is an obvious indicator of declining coral health and potential stress on the reef ecosystem. Effective field-based monitoring and reporting systems are established in many regions to identify and respond to disease outbreaks (Beeden et al., 2012). However, the underlying causative agents, either biotic or abiotic, of many coral diseases have been difficult to identify because the drivers of outbreaks may be linked to multifaceted interacting effects of environmental stress, reduced host fitness, destabilized symbiosis within the coral holobiont, and increased abundance or virulence of microbial pathogens (Bourne et al., 2009; Burge et al., 2014; Mera and Bourne, 2018; Woodley et al., 2016). These difficulties are highlighted by the recent extensive mortality of a number of coral species due to an ongoing disease epidemic in southeastern Florida for which the underlying causes still remain unknown (Precht et al., 2016; Rippe et al., 2019; Walton et al., 2018). Because many restoration approaches are dependent on disease-free corals before intervention (e.g., managed breeding, assisted gene flow) plus avoiding losses due to disease after intervention (e.g., algal symbiont manipulation), or spreading disease agents across geographically dispersed areas (e.g., managed relocation with introduction to new areas), research into coral diseases, their vectors, and treatment remains an ongoing priority.

Elucidating underlying coral disease etiology to allow rapid identification of the underlying causes and implementing measures to manage, prevent, or mitigate spread is a priority. For interventions such as antibiotic treatment, knowledge of the specific pathogen(s) and their mode of action is critical to provide informed choices for which antibiotics will be effective, where to target application, and when to apply the treatments. Similarly, phage therapy treatments can only progress when the target host bacterial population is identified, and effective application is dependent on knowledge of the infection process. Disease is generally an interplay between the

causative agent (biotic or abiotic), the host, and the surrounding environment. Therefore, at the heart of disease causation is the host response to challenge, and in the case of corals, their immune system is surprisingly complex for an organism with a relatively simple tissue organization (Mydlarz, 2019; Mydlarz et al., 2010; Palmer, 2018; Palmer and Traylor-Knowles, 2012; Toledo-Hernández and Ruiz-Diaz, 2014). Recent studies have significantly improved understanding of the coral immune system (Mydlarz, 2019; Palmer and Traylor-Knowles, 2012; van de Water et al., 2016), however identifying the response of this immune system to disease onset is a significant knowledge gap. In undertaking restoration of reef ecosystems, preventing or mitigating effects of disease will be paramount and aided greatly by improving the knowledge of the underlying factors contributing to disease and the corals' response at all life stages (planktonic larvae, juveniles, and adults).

Finally, the goal for many intervention programs is likely to be the maintenance of coral reef structure and function as it is associated with the sustainable delivery of associated ecosystem services. Monitoring whether intervention programs achieve this goal will require indicators of ecosystem "health." These indicators can also inform prioritization of locations for testing and deploying interventions based on the degree of reef degradation as described in Chapter 2 (T. Smith et al., 2008). A large array of possible indicators range in ecological scale (e.g., the coral community, the associated fish and invertebrate community, the social system) and metrics (e.g., cover or biomass, rugosity, species richness, evenness, functional diversity). A research challenge is then determining which indicators best predict larger-scale processes, such as system-wide resistance to and recovery from disturbance to maintain a coral-dominated state (e.g., McClanahan et al., 2012), that connect to the ecosystem health goals identified by stakeholders.

3. Determine functional roles of, and tradeoffs among, members of coral reef communities at multiple ecological scales from coral-associated symbionts and microbiomes up to the composition of coral species in reef communities

The symbiosis established between the algal dinoflagellates (Symbiodiniaceae) and the coral host underpins the health and resilience of coral reefs, and this intimate association has been the focus of a large current and historical body of research (e.g., Cowen, 1988; Falkowski et al., 1984, 2008; Suggett et al., 2017). The manipulation of the symbiotic associations has garnered much interest due to the potential ability of these symbionts to increase stress tolerance (van Oppen et al., 2017). While shuffling or switching the algal symbionts is currently possible, the effects are temporary; fast-tracking efforts aimed at filling the knowledge gaps would help facilitate successful future restoration activities and reduce risks associated with symbiont manipulations at this pre-intervention stage.

The other microbial communities associated with corals (bacteria, archaea, fungi, and viruses) also play important roles in maintaining coral health, but understanding of this symbiosis lags behind that of the algal-coral association. Whereas there has been extensive research determining the diversity of the coral microbiome, understanding is still limited regarding the function that the microbiome plays in the holobiont and which interactions are essential to health and stress resistance. This includes if there are shared metabolic pathways for the coral, algal and microbial partners, and the spatial integration (niche micro-habitat localization) of these communities

within the coral animal as a whole. Manipulation of these other microbial symbionts has been proposed as an additional means of conferring stress tolerance to corals, and the research gaps overlap somewhat with Symbiodiniaceae manipulation questions.

The major research priorities for manipulation of algae and other microbial groups in symbiosis with coral include identifying the suite of taxa that can provide the required conferred traits of tolerance to the host (including tolerance to varying environmental stress plus disease resistance) and how these associations can be managed. For these populations, identifying their required abundance, their specific functions, and the mechanisms that confer benefit to the coral holobiont is an ongoing research priority. The specificity and flexibility of these associations over multiple symbiont types and coral species need to be established with a focus on corals targeted for restoration. In addition, elucidating the direct versus the indirect effects of algal and microbiome symbiont manipulation on the coral host is needed. For example, does adding or shifting a microbial community member(s) benefit the coral host by a specific inferred trait (i.e., ROS scavenging) or is it simply stimulating other processes, such as adding nutrients that stimulate a microbial loop and hence coral heterotrophic feeding (i.e., no association is established with the coral host)? Additionally, the longevity of association of introduced symbionts within the coral host, and if these associations can be maintained across generations, need to be determined to guide when and how often interventions to shift the symbionts and/or microbiome to increase resilience (or more temporary stress tolerance) is required. Lastly, improved understanding and assessment of tradeoffs for each individual coral species/symbiont manipulation is essential because this will inform us of the associated risks of algal and microbiome symbiont manipulation.

Finally, the genetic, reproductive, physiological, population, and community interventions require identification of a target coral species or set of species. Informed prioritization of target species to achieve a goal of maintaining coral reef ecosystem function will rely on identifying the functional role of different coral species (e.g., Darling et al., 2012) and the vulnerability of different functional groups and life history types (e.g., Darling et al., 2013; McClanahan et al., 2014; van Woesik et al., 2012). Such prioritization can further rely on an understanding of the tradeoffs between tolerance to different stressors as well as between different life history types and functional roles. This includes the relative roles of the most stress-tolerant types (Côté and Daring, 2010), as compared to a diversity of functional types (Baskett et al., 2014), in overall reef persistence in a high-stress future.

4. Identify population structure, determine evidence for local adaptation, and define relevant management units for population recovery.

Understanding the standing genetic variation in corals is critical to defining the genotypic diversity, distribution, and connectivity between populations within a species range. Such information is central to many interventions that involve the collection, outplanting, and translocation of individuals. Ideally, this information would be gathered through population genetic studies and measures of ecological connectivity across metapopulations, such as the range of larval dispersal and recruitment and the speed of any range shifts that are naturally occurring. Additional information is also required on the extent of local adaptation across the species range, and the performance of different genotypes across a range of environments that

emulate future climate projections. This information might be obtained through common-garden experiments that use a broad range of genotypes representing each of the populations or environments compared. Similarly, the population genetic structure of critical symbionts, such as Symbiodiniaceae, may need to be considered both in terms of their functional role (Parkinson et al., 2015), and as part of translocations (Grupstra et al., 2017), given that they introduce novel variation to local populations and may invoke many of the same concerns considered for coral host populations.

Information on population structure is relevant to the hierarchy and scale at which interventions should be conducted. Risk assessment requires an understanding of the effect an intervention might have on rebuilding within populations, as well as the impact that interventions might have on metapopulation structure as a whole. Risk assessments might also seek to understand how specific interventions impede or enhance adaptability of coral reefs into the future—for example, whether individuals translocated across different populations enhance or reduce persistence. In this case, biologically relevant information on local adaptation will help identify optimal source and target populations. It is also worth estimating the genetic variability, genetic load and fitness of edge versus central populations, because the former may be the target for conservation actions (e.g., whether assisted gene flow from the center of a species distribution might be an effective restoration approach).

Management units for target species are central to conservation planning. In the United States, the definition of management units relies on information on population structure and on evidence of adaptation (Waples, 2006). The latter is often challenging to define and might include proxies such as selective regimes (differences in ecological and environmental variation) and phenotypic or life history diversity. The definition of management units informs the development of appropriate status reviews (Brainard et al., 2011), risk assessments (Boyd et al., 2017), and recovery planning (NOAA, 2015). They also inform the context of decision making, by defining the jurisdictional boundaries and identifying the stakeholders and decision makers that will be engaged in the recovery process. Definitions of conservation units have been prioritized in corals broadly (Brainard et al., 2011), but require fine scale development within key indicator species.

5. Develop methods to improve survivorship for corals that are released, planted, relocated, or settled on reefs, at the reef scale.

Increasing the survival of corals that are reared, planted, relocated, or settled on reefs is essential for ecologically and financially effective restoration efforts (dela Cruz and Harrison, 2017; Raymundo and Maypa, 2004). For interventions that rely on sexual reproduction, larval recruitment, and juvenile grow out, success at ecological scales requires shifting the survival curve from type III (low survivorship at early life stages) to higher age-specific survival probabilities in early and middle life stages (see Figure 5.1). Population rearing and release will likely be conducted not only for genetic and reproductive interventions, but also physiological and ecological interventions that rely on introduction of treated gametes, larvae, or adults into the water. Rearing should seek to enhance survivorship in culture, while retaining or creating as high amount of genetic diversity as possible and minimizing risks posed by pathogens. Supportive breeding, hybridization, and managed selection rely on rearing methods that reduce the impact of the culture environment as well as on release strategies that improve survivorship in the wild.

Certain physiological interventions require appropriate rearing environments for pre-exposure or delivery, which in turn rely on culture environments that are conducive to such methods.

The development of appropriate release strategies for larvae should aim to improve settlement cues and optimize benthic substrates that enhance coral larval recruitment and subsequent survival (e.g., managing algal turf; Arnold et al., 2010). These factors have been studied for only a select few coral species; universal settlement cues and optimized substrate conditioning is an important pre-intervention step for many restoration approaches. Post-release survival can be low (50-100% mortality can occur in the first five years; Young et al., 2012) such that an understanding of the relative and interactive effects of different abiotic and biotic drivers of near-term survival of outplanted corals (e.g., degree of wave shelter, prevalence of corallivorous snails and fireworms, presence of herbivores that can mitigate competition with macroalgae) can inform methods for improved release success (e.g., identification of locations for release, corallivore clearing, herbivore reintroduction; Idjadi et al., 2010; Young et al., 2012). For interventions that rely on propagating individuals both within populations (from high stress environments) or between populations (managed relocation), improvement in methods of transportation, banking of large numbers of individuals, and increased survivorship of the relevant life history stage (such as coral fragments or gametes, including cryopreserved gametes) are required. Resultant technologies need to be adapted for both large-scale aquaculture operations that supply coral for outplanting, as well as performing in situ reef-scale applications. Finally, while cryopreservation approaches are successful for many coral species (Daly et al., 2018), developing approaches for egg storage and egg revival that allows subsequent fertilization and large-scale supply will greatly help the approaches detailed above.

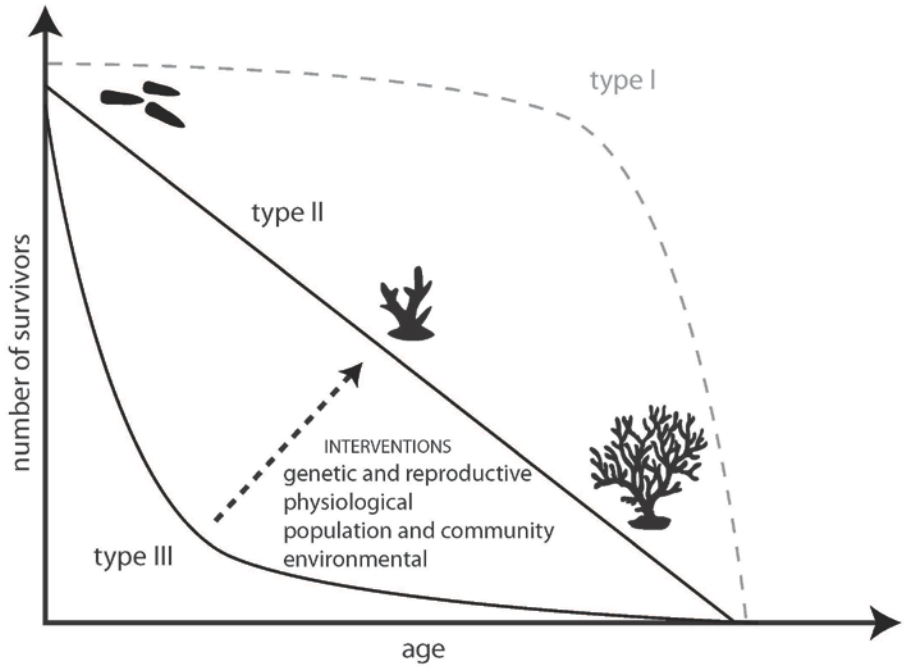


Figure 5.1 Graphical depiction of a desired shift in survivorship from type III (low survivorship at early life stages) to type II or type I as a result of intervention implementation. CREDIT: Hillary Smith, James Cook University.

6. Develop extensive, freely available databases on coral communities, hosts, symbionts, and microbiomes to support studies on genotype-phenotype relationships, population structure, and community dynamics.

Genetic markers for target species will play a central role in fundamental coral biology research relevant to interventions, and ongoing monitoring for risk assessments. Such markers are required for defining population structure; for identifying genotypes held in captive breeding facilities and determining strategies for outcrossing; and for determining the survivorship of individuals in technologies that rely on gamete and larval seeding, sexual reproduction, and relocation. Advanced genomic and other "omic" approaches can assist investigations into the extent of local adaptation, although this work needs to be substantially extended from present efforts. Genetic manipulation requires extensive characterization of the genotype-phenotype relationship of corals and symbionts in different environments in order to identify genes that may be manipulated to confer resilience. Interventions that rely on population structure and monitoring recruitment success require fewer markers than those that depend on a greater understanding of the genome and its interaction with the environment. The development of whole genome resources for target species will benefit all efforts.

Given the high value of coral genetics and genomics data for the design of intervention strategies, significant effort needs to be expended in this area, targeting a variety of ecologically important species. The panoply of "omics" methods (e.g., genomics, transcriptomics, proteomics, metabolomics, methylomics) available in modern scientific research holds great promise in uncovering the genetic basis of phenotypes, and with the advent of genome-editing methods such as CRIPSR/Cas9 (Cleves et al., 2018), the opportunity to validate and/or enhance gene function. These methods have been applied to corals and their dinoflagellate symbionts, and a variety of key genes and pathways related to stress responses have been identified (Guzman et al., 2018; Helmkampf et al., 2019). However, given that typical corals contain in excess of 20 thousand genes and responses to stressors such as elevated temperature can lead to the differential expression of hundreds to thousands of genes (Shumaker et al., 2019), identifying individual targets for genetic manipulation remains a major hurdle in this field. This complex biological system would benefit from a rapidly expanding arsenal of bioinformatic methods referred to as multi-omics. These approaches aim to integrate multiple lines of "omics" evidence and other forms of data such as protein-protein interaction networks to explain phenotype (e.g., Huang et al., 2017; Kim and Tagkopoulos, 2018). Shared network hubs derived from different "omics" datasets can provide strong evidence for genes that underlie a particular phenotype. Data or network integration provides, therefore, the framework to move beyond analyzing single data types. These methods require, however, that inferences are grounded in the biological world and have ecological importance, rather than being exhaustive catalogues of species or gene expression and metabolite data (Vilanova and Porcar, 2016). Multi-omics is poorly developed in corals, and once such data are produced and made freely available in public databases, it will still require extensive testing in natural conditions to identify the major players (genes, pathways) that underlie coral stress tolerance and resilience. However, once these types of data are available (e.g., as in the mouse model; Li et al., 2018), then the choice of regulatory genes for targeted manipulation using genetics (i.e., through under- or over-expression) will have a firmer foundation. Equally important will be the collection of abiotic data at the level of individual coral genotypes to allow the discovery of loci that may confer specific adaptive traits. The current use

of reef or broader site-level measurements will therefore need to be scaled down to the level of colonies with sensors that are both inexpensive and powerful (e.g., Sekli Belaïdi et al., 2019).

Beyond "omic" databases, support for databases of life history, phylogenetic, and biogeographic data (such as the Coral Traits Database; Madin et al., 2016) will be central to informing multiple decisions around interventions. Life history and phylogenetic data can inform identification of target species based on possible stakeholder priorities such as phylogenetically unique species and species with particularly vulnerable or invulnerable life histories (see Research Need #3). Phylogenetic data can also inform the drivers of species ranges and local adaptation within those ranges, which will be particularly important to informing decisions on translocation-based interventions (see Research Need #4). Finally, all data types can lead to more rapid development and parameterization of models that inform the decision-making process as described in Chapters 3-4: biogeographic data can identify the relevant species to consider modeling, life history data can provide parameters for those species, and phylogenetic data can help identify parameters for closely-related species when data for a given target species are not available.

7. Identify species-specific threshold responses of corals to changes in temperature, light incidence, and ocean pH, as well as reef-scale threshold responses to disturbance and environmental change.

Interventions are most necessary in areas where corals will experience environmental conditions in which they have a low likelihood of natural adaptation or acclimation. Just as predictions of future environmental conditions are important for assessing the benefit of deploying an intervention, so is understanding the response of corals to these conditions. Increases in average temperature of 1-2°C can lead to coral bleaching (Donner et al., 2005; Frieler et al., 2013; Hoegh-Guldberg, 1999; Sheppard, 2003; van Hooidonk et al., 2013, 2014), although the threshold varies by species. Heat tests based on long-term exposure (multiple days to weeks) to low levels of heating (1-2°C above ambient) are common in the bleaching literature (Ainsworth et al., 2016; Jokiel and Coles, 1990; Lesser, 1997; Oliver and Palumbi, 2011). In addition, more rapid acute heat tests have been used comparatively among species and individuals within species (Barshis et al., 2018; Morikawa and Palumbi, 2019; Parkinson et al., 2018). However, for mapping heat tolerance (and sensitivity) to improve the parameters for modeling and reduce uncertainties, the methods for assessing bleaching thresholds need to be standardized across coral species and conducted for corals inhabiting specific target reefs. Development of a standardized, inexpensive, low maintenance, reliable temperature control and experimental system that can deliver a variety of temperature profiles would be a key goal.

Harder to quantify is the potential amount and rate of coral adaptation to increased thermal stress through the interactive effect of multiple mechanisms, which is necessary to understand the impact of various climatologies on coral survival. Therefore, improving measures of species susceptibility and mechanisms of increased thermal tolerance that can be integrated into the modeling approaches and reconciled with physiochemical metrics such as degree heating weeks (DHW) will inform prediction of differential loss of species due to temperature driven ecosystem stress. Because there are multiple mechanisms that could lead to increased tolerance over ecological timescales, it is also important to investigate how these mechanisms could interact to constrain or facilitate adaptive evolution (e.g., Ghalambor et al., 2015; Kronholm and Collins,

2016). Species-specific susceptibility and adaptability metrics across other environmental stresses (i.e., nutrients, light, pH) would further resolve the predictive value of modeling efforts. Being able to quantify these coral species-specific responses to environmental change would importantly assist in identifying when environmental interventions, which reduce stress experienced by coral, would have an impact on coral survival or increase the benefit of other coral interventions.

In addition to physiological response and adaptive capacity to environmental stress, a mechanistic understanding of population- and community-level response to environmental stress will inform a strategy of protecting overall reef resilience (Anthony et al., 2015; McLeod et al., 2019). Understanding the mechanisms that support the maintenance of a coral-dominated state during and after disturbance (e.g., relative roles of factors such has diversity, connectivity, and the degree of different local stressors) can (a) inform modeling and selection of local management actions that might increase reef persistence and therefore intervention success (b) inform where and how much interventions might alter overall resilience. Coral population- and community-level response to disturbance might depend on thresholds in coral diversity and cover necessary for reef-level persistence. On the population level, thresholds in coral population density and genetic diversity might affect successful reproduction (where diversity could affect reproductive success for obligate outcrossing species; Baums, 2008; Miller et al., 2018). On the community level, thresholds in overall coral cover and community composition might affect the maintenance of a coral-dominated reef state with high herbivory on macroalgae (Mumby et al., 2007; Bellwood et al., 2004). The potential for community-level thresholds is particularly controversial and unresolved given the long timescale of observations necessary to discern their relevancy to ecological systems (Mumby et al., 2013; Petraitis and Dudgeon, 2004; Żychaluk et al., 2012). Discerning whether or not population- and community-level thresholds are relevant, and if so, what the threshold values are is vital to identifying locations where interventions are more likely to be successful and the scale of interventions that might be necessary for success (see also Research Need #9).

SITE-SPECIFIC RESEARCH AND ASSESSMENT TO DETERMINE WHETHER INTERVENTION IS NEEDED OR POSSIBLE

Development of appropriate ecological models and identification of relevant management objectives and goals require site-specific information. The following research areas include the research and assessments that should be conducted to inform robust decision-making processes including identifying the problem, developing managing objectives and evaluation metrics, and modeling risks and benefits. The goal of such research is to evaluate which interventions might be appropriate in a particular setting (if any), how they would be implemented, and what objectives they could be expected to achieve.

8. Identify local stressors that influence population recovery and determine whether stressors are likely to influence the success of the intervention.

As the committee illustrates in their model in Chapter 4, it is important to integrate the impact of local stressors (and management of these stressors) into a decision framework to evaluate the use

of the more novel coral interventions as part of a comprehensive management strategy. Reef degradation is often the result of multiple stressors on the ecosystem acting synergistically (Gardner et al., 2003; Hughes and Connell, 1999; Hughes et al., 2017b). The effects of local impacts such as poor water quality, coastal development, and overfishing are well documented (Fabricius, 2005; Jackson et al., 2001; Mora, 2008), and unless these stressors are managed effectively the benefits of any proposed intervention may be minimal. For example, recent work identified that the resilience of coral populations was impacted by poor water quality, because the recovery following a disturbance is much slower and populations are more susceptible to other localized impacts such as higher predation and disease (MacNeil et al., 2019). Similarly, the appearance of the Stony Coral Tissue Loss Disease in Florida and parts of the central and northeastern Caribbean (NOAA, 2019) highlights important considerations when assessing which interventions may or may not be an option. In this case, managed relocation may not be a viable option (without additional strict quarantine measures). Hence, knowledge of the historical, current and predicted future local stressors is required to assess if any proposed intervention can be successful and meet the goals of the project.

9. Develop appropriate metrics and recovery goals that assess the effects of the intervention on ongoing tolerance, health, fitness, and recruitment within the target management unit as well as on connected reefs.

Risk assessments and monitoring efforts depend on accurate measures of community composition and population demographic data, such as survivorship and recruitment, within the specific environmental context. Therefore, accurate baselines and appropriate metrics need to be established before the interventions are implemented. Data collection specifically targeted at characterizing community composition and interactions is essential, because not all corals will respond to interventions in the same way. Defining demographic patterns for target species within the local context will also inform programmatic decisions on whether interventions are effective in meeting recovery goals, especially in the context of a changing environment. Therefore, it is important to determine which community measures and species-specific traits are relevant to population recovery parameters—for example, reef structural complexity as it relates to multiple reef functions (Graham and Nash, 2013), algal cover, and multiple coral attributes, such as diversity, cover, growth rate, reproductive rate, disease susceptibility, and thermal tolerance.

As noted in Research Need #7, the success of interventions that involve outplanting, such as managed breeding and managed relocation, might depend on population- and community-level thresholds in values such as genetic diversity (Baums, 2008; Miller et al., 2018) and coral cover (Mumby et al., 2007) necessary for reproductive success and reef-level persistence. Quantifying such thresholds can identify the appropriate targets for restoration of ecosystem processes (Mumby et al., 2007; Suding and Hobbs, 2009; Suding et al., 2004). Therefore, the development of metrics should take threshold effects into account where they are expected to be relevant.

Finally, it is also important to understand how an intervention on one reef may impact the demographic properties of adjacent reefs. Setting target population sizes for species of interest is part of this effort; as population size increases, so may recruitment on adjacent reefs. Therefore, site-specific research should be conducted to determine connectivity between a target reef and

adjacent reefs. Understanding the degree of connectivity from other reefs to a target reef can also inform evaluation of whether or not relocation (assisted migration and assisted gene flow) can improve on naturally-occurring dispersal and range shifts.

10. Evaluate whether population recovery at a specific site can be achieved through managed relocation or managed breeding and if so, which intervention is most appropriate for recovery.

In cases where the objective is to supplement reef populations with more individuals, the preferred intervention strategy will depend on a balance between the risk and the likelihood for recovery. In all cases, assessing the impact of broodstock collection (whether through fragmentation or collection of gametes and larvae) on wild or captive source populations is necessary. This information might be gathered through site-specific mapping of coral distribution, measurement of genotype diversity across the reef, and assessment of population size. Similarly, the risk of releases or managed relocations from such programs on target populations should be evaluated by measuring the degree of genetic divergence between the source and target populations and estimating their effective population sizes. The risk to local populations may increase with greater genetic divergence of introduced individuals (whether through inadvertent changes due to domestication or to deliberate manipulation), especially following reproduction between the source and target populations. However, this risk should be balanced against decreased genetic divergence and adaptability in the target population, especially given a rapidly changing environment.

11. Identify host, symbiont, and microbial populations at target restoration sites to ensure treatments or manipulations aimed at improving coral physiological performance can achieve recovery goals.

Physiological response of coral populations to environmental conditions can be attributed to the host, the symbiont, and/or the microbiome. Therefore, identification of available symbionts (including the microbiome) and their potential beneficial traits is needed at each site. This includes establishing the diversity, specificity, and flexibility of these associations over multiple symbiont types, microbiome populations, and coral species. Having a good understanding of the host-symbiont dynamics through a multispecies genetic modeling framework will help to disentangle the role of diversity in the efficacy of interventions and improve the predictions of the responsiveness of the coral to interventions. For example, pre-exposure treatment aimed at conferring some degree of additional tolerance to subsequent re-exposure requires understanding of the response of populations and the potential mechanisms that contribute to increased tolerance across the host, symbiont, and microbiome. Similarly, for other physiological treatments including antibiotics, antioxidant, nutritional supplementation, and phage therapy, assessment of effects on the host and changes in community structure across the symbiont and microbiome populations before and after treatment is required and needs to be linked to individual and reef-wide coral health metrics.

Relatively little is known about the diversity, community structure, and abundance of free-living Symbiodiniaceae in reef waters and sediments, or the degree to which corals acquire symbionts from these sources, or exchange them with other non-coral hosts. Changing environmental conditions may shift the relative abundance of different symbionts, and local declines or

extinctions of coral hosts will likely also affect the availability of appropriate symbionts. This in turn may impact recovery/repopulation dynamics and potentially limit the capacity of reef corals to respond to changing conditions. Consequently, a greater understanding of the population dynamics and genetic diversity of algal symbionts among different hosts and free-living life stages is required.

12. Assess in a site-specific manner the benefits, risks, and chances of success for implementing environmental interventions.

Each reef site or region needs to be assessed for its physical suitability for the proposed intervention. All environmental interventions are dependent on a set of bathymetric, geomorphologic, oceanographic, and/or atmospheric conditions to be met for the intervention to have a chance of success. Without meeting these defined geophysical parameters, the risk of failure and unintended consequences for the intervention increases.

The environmental interventions can operate over different scales. Most proposed interventions are at the reef scale (increased turbidity, shading layers, microbubble ocean whitening, mixing of cool waters, abiotic and biotic ocean acidification interventions) potentially focused on high value reefs, though atmospheric shading (marine cloud/sky brightening) can operate over regional scales. Infrastructure costs associated with implementation is a major barrier for many of these intervention strategies (i.e., shading using physical structures, mixing of cool water, or marine sky brightening). For some reef scale interventions (increased turbidity, polymer shading layers, microbubble ocean whitening, mixing of cool waters, chemical additions), modeling that provides detailed water residence and flow dynamics across the reef is required. Similarly, for the use of seagrass meadows and macroalgal beds to reduce ocean acidification, the foremost limitation is identification of geographic setting, reef type and oceanography that allows it to be effective. Hence, site specific and robust, linked biogeochemical, biophysical and hydrodynamic models are required on a site by site basis to assess suitability and the probability of success of the intended intervention (e.g., cloud brightening by Alterskjær et al., 2012; biotic ocean acidification interventions by Anthony et al., 2013).

13. Identify the most appropriate site-specific, synergistic management and intervention strategies that together provide greater chance of success and reduced risks than the sum of the impacts of each intervention alone.

The benefits and risks associated with interventions to increase the resilience of corals and reef ecosystems have been addressed individually (NASEM, 2019). However, it is clear that many interventions are synergistic; the benefits of implementing two or more approaches increase the chances of success of each and cumulatively provides even greater potential reef resilience benefits. It should also be noted, however, that some combinations of interventions may have antagonistic outcomes and these risks need to also be assessed. The modeling framework in Chapter 4 details an example of a dynamic coral reef model to illustrate how one might use the output in a decision-making process. For this example, traditional management of herbivores was assessed with assisted gene flow and atmospheric shading. However, empirical data that identify the synergies between both traditional management and the array of novel intervention strategies are a necessity, and to date have not been collected at any scale. Some reef systems might need

specific combinations of interventions to achieve success (i.e., active algal removal prior to larval capture and release). Nevertheless, research that specifically assesses these synergistic benefits (as well as potential antagonistic interactions) between traditional management approaches in conjunction with novel intervention strategies is vital to reduce uncertainty associated with the outputs of the modeling approaches.

RESEARCH TO IMPROVE ASSESSMENT OF THE BENEFITS, EFFICACY, AND RISKS OF SPECIFIC INTERVENTIONS

Research is needed to stage interventions from laboratory experiments to full-scale management strategies so the safety, efficacy, and cost-efficiency of interventions can be improved. Implementation of a research program around risky approaches may benefit from a phased testing program, where decision points occur that require stakeholder-based criteria to progress in a step-wise manner from the laboratory to the field (such as is recommended for gene drive research in NASEM, 2016 based on WHO, 2014). Other approaches may have more well understood risks and benefits but require a development program to design effective implementation. For example, while interventions such as probiotics (microbiome manipulation), antibiotics, and nutritional supplementation are possible, they lack specificity due to limited understanding.

14. Develop protocols for control of pathogens (biosecurity and quarantine).

Biosecurity and quarantine protocols are important for identifying, isolating, and removing pathogenic microbes. Such protocols have been developed for many jurisdictions and countries (Hathaway and Fisher, 2010; Hewitt and Campbell, 2007) and are priority for industries such as the marine aquarium trade (Morrisey et al., 2011) and high value aquaculture farms (Palić et al., 2015). However, similar robust biosecurity and quarantine protocols need to be adapted to meet the requirements of the expanding reef restoration activities, incorporating the additional challenges that arise from the emerging intervention strategies highlighted across this report. Many coral restoration approaches rely on assessing the pathogen loads and virulence potential within coral populations and preventing their further spread. Large-scale aquaculture operations can promote increased disease occurrence due to high population densities and suboptimal environmental conditions. Managed breeding and managed relocation interventions also have the potential to spread disease. Through improved understanding of the underlying etiology of coral diseases, development of rapid diagnostic assays for the identification of pathogens and quantification of their abundance and/or virulence is possible and should be a long-term goal of disease studies to reduce risks associated with intervention approaches (Pollock et al., 2011).

Corals are also host to a wide range of other cryptic organisms that interact across the mutualism-parasitism continuum (Bronstein, 1994). These organisms, which may include but are not limited to acoels, digeneans, polyclads, gastropods, decapods, copepods, and pyrgomatids, can be hosted by corals in low abundance in natural environments but become problematic under captive conditions or when moved to environmental ranges that do not also host natural biocontrol organisms. Hence, a more comprehensive understanding of the cryptic species

associated with corals, their symbiotic interactions and their potential for causing detrimental effects on individual corals or the ecosystem more widely is warranted.

15. Develop effective approaches to modify symbiotic algal and/or microbiome populations.

Though conferred beneficial stress-tolerance traits have been detected for some algal symbiont populations associated with coral (Suggett et al., 2017) and potentially for the microbiome (Rosado et al., 2018), there are currently no effective approaches to modify these algal and/or microbiome populations or shift the abundance of members of these populations at a scale that would help confer benefits to multiple coral species. Having approaches that are effective at shifting populations, are targeted to specific populations (host, symbiont and microbiomes), and do not result in detrimental effects on the target corals (known as dysbiosis), is critical to reduce associated risks for these interventions. The longevity of the symbiont populations and their associated conferred traits (including across generations) with the coral host needs to be established to inform whether manipulation and therefore delivery of the modified symbiotic communities is a periodic intervention during times of stress. If manipulations are undertaken during coral settlement and juvenile grow-out in aquaculture facilities, the long-term maintenance of a modified symbiont community and the ongoing conferred traits needs to be established in situ.

16. Develop effective approaches to determine whether corals that are released, planted, relocated, or settled on reefs contribute to recovery goals, while reducing risk to ongoing adaptation and ecological processes.

Risk assessment based on evolutionary principles requires the development of models to assess the impact of gene flow from introduced corals on the genetic diversity of established populations, which in turn influences population demographic processes (Baskett and Waples, 2013; Ford, 2002; Lynch and O'Hely, 2001; Tufto, 2017). Benefits and risks associated with gene flow relate to changes in effective population size, rates of inbreeding, and fitness. Risks associated with the first and second factors might occur through large releases of individuals with little genetic diversity, or by limited recruitment. The third may result following introduction of maladapted individuals and interbreeding between such individuals and native corals. Each of the interventions within this category will benefit from research that evaluates the genetic gains versus risks associated with each activity, as well as the associated changes in population growth and recruitment.

Supportive breeding propagates a portion of a population using local broodstock, and releases these individuals back into natural environment. Genetic gains may be accrued by increasing the effective population size, increasing genetic diversity through reproduction, and improving the population’s ability to adapt. However, if insufficient diversity is captured by the breeding program, then genetic change might occur through a decrease in effective population size and inbreeding, or domestication selection. This change may in turn compromise health of the wild populations. Therefore, research should evaluate the genetic diversity within the captive and wild populations, and monitor long-term fitness changes in the supplemented population. Managed selection, outcrossing between populations, and hybridization between species are intended to increase genetic variation and fitness of released individuals, especially in changing

environments. However, research in this area is limited to a few case studies, and often to laboratory settings. Scaling these interventions to the natural environment depends on concerted efforts to evaluate offspring performance in the target environments. Risk assessments need to evaluate whether released individuals pose an ecological or genetic risk to existing populations, and whether they contribute to population growth. Relocated corals, or corals with novel genotypes, may interbreed with individuals in target populations or with themselves. Fitness benefits seen in one generation may not be transmitted to the next, which in turn may affect population growth and survival. This information is thus relevant to risk assessments that evaluate recovery goals across generations, especially when non-native or domesticated genotypes are introduced.

Finally, it is necessary to investigate how the number of introduced individuals affects intra- and inter-species interactions and ecosystem functioning. Risk assessments that combine genetic models with demographic models may include density dependence, competitive interactions, and changes in community composition through interactions with other species such as symbionts, fish, and macroalgae.

17. Develop and test genome-editing methods in a wide variety of ecologically important coral species.

As with all multicellular organisms that house a complex microbiome, targets for genetic manipulation in corals are not only difficult to identify, but the outcomes of genetic changes are challenging to predict. Nonetheless, the first trials of CRISPR/Cas9 methods have been completed in coral animals (Cleves et al., 2018), resulting in mosaic creation of tissues containing gene deletions or knockouts. There is as yet, no evidence provided of an altered phenotype or the inheritance of edited genes in adult corals. These technical issues may be addressed in the near future, but developing or identifying faster growing (e.g., shorter generation time) corals would also be a major advance in this field. However, even if the incorporation and complete or near complete inheritance of edited genes can be proven in adult coral animals using CRISPR or other methods (e.g., transcription activator-like effector nucleases, TALEN), it is unclear how effective these methods will be in field trials. Nonetheless, given the high promise of genome-editing methods to enhance coral resilience through stress-tolerance, there is a clear need to develop and test these methods in a wide variety of ecologically important coral species for deployment in the future.

In contrast, no genome-editing or genetic-transformation methods have yet been published for the algal symbionts of corals. Although the microbial component of the coral holobiont (the microbiome) is known to play an important role in reef health, genetic manipulation of these microbes has also not yet been attempted. A major research need in this area is identifying the major genes and pathways involved in coral holobiont resilience under fluctuating environmental conditions. Identifying the most useful phenotypes to be used for genetic selection that are relevant to “real world” conditions is also a priority. In addition, development of more robust genetic modification techniques for the coral animal to efficiently spread adaptive genes into natural populations is required alongside accelerating the life history of corals to allow more generations to be produced and studied prior to out-planting. Finally, developing genetic tools for the algal symbionts of corals should be facilitated.

18. Develop methods of delivery for nutrients, probiotics, antibiotics, phage therapy, and antioxidants at reef scales.

Some proposed interventions that promote coral resilience can be combined, provided appropriate reef-scale delivery approaches are developed. For example, nutritional supplementation of corals can be linked to provision of probiotic coral microbes, antioxidants, antibiotics, and phage therapy. Developing coral specific diets that promote increased fitness through enhanced heterotrophic feeding can also contain antioxidants and symbionts (algal and microbial probiotics) that confer benefits to the coral host. Scale of production for such supplements is easily achieved but what is required is improved knowledge of the nutritional requirements of coral (Conlan et al., 2017) and conferred benefits for each coral species that increases resilience. Constraints on heterotrophic feeding exist for different coral species, with some corals possessing large polyps well suited to capturing prey to supplement their diets while other coral species have small polyps and rely heavily on photosynthesis-derived nutrients rather than heterotrophic feeding. Hence, for coral species targeted for restoration, feeding dynamics and nutrient acquisition and energy budgets need to be refined.

Formulation of diets, inclusive of probiotics, is well developed in the animal and human therapeutics industries and possibly transferable to corals. For example, encapsulation of probiotics and antioxidants into digestible formulations is a global multi-billion-dollar industry (Sapkale Anita et al., 2012; Shinde et al., 2014). Adapting these approaches to develop formulations that can deliver nutritional supplements, probiotics, antibiotics, and antioxidants to corals is a research priority provided the benefits are demonstrable. Delivery of such formulations is easily achieved in experimental systems or large-scale coral aquaculture facilities. However, delivery onto reefs and at the ecosystem scale is much more challenging. Whereas it is conceivable to deliver encapsulated formulations onto a reef, ensuring these bundles target corals specifically and are ingested or taken-up is far more challenging and associated with risks such as enhancing nutrients entering the reef and stimulating growth of undesirable reef communities such as macroalgae.

19. Assess feasibility, potential benefits, costs, limitations, and risks associated with environmental interventions.

Currently, the effectiveness and potential benefits of the proposed environmental interventions can only be derived theoretically because there are few operational examples that conclusively demonstrate an increase in coral resilience over any scale. Though a small field trial is being conducted on the Great Barrier Reef for bringing deep water to the surface to cool reefs (Reef Havens Project, https://www.rrrc.org.au/reef-havens/) there is still insufficient information from this project and for all current proposed environmental interventions. Hence, further small scale experimental and field trials are a priority in these areas to assess feasibility, potential benefits, costs, limitations, and the risks.

Many of the environmental interventions require significant technology development that can be adapted for application in reef ecosystems. For interventions such as atmospheric shading and cool water mixing, the challenges lie in the design, engineering, and deployment of equipment and infrastructure to ensure they are feasible and effective at their desired scale of impact. Cool

water mixing can be targeted at the reef scale, whereas atmospheric shading is expected to have impacts at a regional scale. Shading that uses thin layer barriers needs demonstration of the effectiveness of these formulations to ensure they are biodegradable and safe, yet also reduce light enough to benefit corals. For all environmental interventions, the general requirements of research, development, and testing is still a priority to determine their effectiveness, control, and technical aspects of scaling up.

RESEARCH TO INFORM RISK ASSESSMENTS AND MODELING

The adaptive management cycle requires monitoring and evaluating the results of a management action based on an established monitoring program in order to iteratively gain information to support decision making. Thus, continuous improvements to a structured decision-making process requires efforts in the areas of monitoring and feedback into model improvements. As described in Chapter 3, there is also a feedback in the reverse direction, where structured decision frameworks can help prioritize areas of research.

20. Targeted monitoring to evaluate performance, improve benefits, and minimize or manage risks.

Though there are a large number of unknowns related to coral interventions, this does not mean action must be delayed. Action can take place based on the best-available science and then monitoring can focus on these key unknowns to resolve them and learn in an adaptive management process (Holling, 1973; Walters, 1986; Walters and Holling, 1990). Any intervention that is conducted for coral reefs will rely on monitoring coral populations and broader reef ecosystems to assess effectiveness of the approach and to identify any unintended consequences. For effective comparisons, baseline information of reef habitat needs to be established at the sites of interventions, and best practices for long-term monitoring regimes need to be implemented. Across the spectrum of all interventions, current established metrics of reef health are important to assess their impact on reef species and the ecosystem more broadly. These metrics relate to management objectives as reflected by the decision criteria, and can include such attributes as coral cover, species diversity, genetic diversity, productivity, disease prevalence, bleaching thresholds, fecundity and recruitment data, and coral growth rates. Additional decision criteria may include social or economic factors.

Often, measures of ecosystem impact and effectiveness of the intervention strategies may be long term. Therefore, establishing intermediate indicators or proxy indicators for whole ecosystem response and impacts is important. Development of robust biomarkers of coral health has been identified previously as a research priority (Research Need #2), and further, technology development that allows incorporation of these biomarkers into small, inexpensive, and portable tools to assess stress tolerance would be highly valuable. Indicator taxa can also be a valuable tool, for example, tracking abundance and cover of macroalgae. Monitoring microbial communities and the tipping points that shift the community can be valuable for earlier detection of ecosystem changes. For example, studies show that anthropogenic stress on reefs can shift microbial communities and their metabolic pathways from autotrophic communities to more inefficient heterotrophic communities that change the nutrient dynamics and flows in the

ecosystem (Dinsdale and Rohwer, 2011; Haas et al., 2013; McDole et al., 2012). Metrics such as microbialization scores have been proposed as one approach to assess changes in microbial function within the reef that directly impacts reef health and resilience (McDole et al., 2012; Haas et al., 2016).

Across all intervention strategies, improved measurement of reef demographic processes will be critical to assess the benefits, identify off-ramps where the intervention may have unintentional consequences, and measure the overall success or failure of the approach. Traditional metrics of changes in coral cover, species diversity, genetic diversity, invasive species, and disease abundance will continue to be effective and central to assessing these demographic processes. However new ways to collect these metrics are being developed and should be embraced; supplementing expensive and laborious diving operations with advanced imaging technologies from satellites, remotely operated vehicles, and underwater drones combined with high powered computing, machine learning, and autonomous technologies, is a priority.

21. Iterative model design to reduce uncertainties and improve model predictions to increase confidence in the decision support framework.

As Chapters 3 and 4 describe and illustrate, model construction, parameterization, and validation for a specific location and set of interventions are intensive but highly valuable endeavors. The previous research items described in this chapter will inform development of the management objectives and provide the data for evaluating management decisions, but further efforts toward model development are required that involve feedback between research/ monitoring and model improvement. Information collected in monitoring programs can reduce uncertainties in biophysical system models by improving parametrization, and by illuminating relationships between parts of the system and between the system and management actions (model structure). The modeling approaches also highlight the uncertainty and the transferability of many interventions from the laboratory and small-scale experimental systems into the field. Therefore, many of the proposed interventions require extensive small- to medium-scale trials to assess the benefit, risks, and scalability, thus informing the knowledge gaps and reducing the uncertainties. This process can require an extensive period of testing and trialing as some approaches need to be assessed over generational times for coral populations. These periods can be as short as two years and as long as ten years for many target coral species. Additionally, the effect of synergistic and antagonistic interactions between interventions, or between interventions and conventional management, on the outcomes of a management strategy will be harder to parameterize in a model until field trials have been undertaken. Hence, to fast track decision processes around restoration, obtaining relevant and informative direct and proxy metrics that can parameterize these decision models is a priority.

Conducting a sensitivity analysis would identify which parameters to prioritize to better constrain the models. Comparing realized outcomes to model predictions informs the adaptive management cycle (see Figure 3.2). This is essential to assess whether the expectations that went into the model resulted in the predicted outcomes. Value of information techniques provide monetized estimates of the value of collecting additional data to reduce uncertainties across model inputs. These techniques can be used to assist in refining monitoring programs and to

identify key biophysical outcomes for which uncertainty is large and having more information would potentially alter the decision.

There is also a critical need to improve/develop higher resolution oceanographic models for target areas of interventions. The model presented in this report is based on coarse resolution SSTs (100km^2; monthly) from a global climate model designed to capture large-scale characteristics of the global climate system (Stock et al., 2011), whereas SSTs most relevant to coral reefs vary at spatial scales of less than 1 km and temporal scales of hours to weeks. Global climate model output should not be applied to make predictions about a specific reef cell. To more accurately represent future coral reef dynamics, global climate models can be statistically or dynamically downscaled or bias-corrected for particular regions (Stock et al., 2011), but additional research is necessary to make linkages between globally modeled SSTs, observed satellite SST measurements, and in situ temperature data. In addition, the thermal environment below the surface of the ocean within the depth ranges of coral reefs is often decoupled from that of the surface, limiting prediction of heat stress with depth (Neal et al., 2014; T. Smith et al., 2016).

RESEARCH CAPACITY

The committee identified research priorities across four broad themes (see Box 5.1). Many are currently established research projects that need to be supported to fast track the goal of developing realistic interventions for reefs faced with multiple pressures. Others require significant research and development within the biology and engineering fields to demonstrate or develop their efficacy for application to reef ecosystems. These research priorities hold significant potential to advance the safe, cost-effective, and scalable approaches to build resilience in coral populations and reef ecosystems more broadly. No doubt the urgent requirement for solutions to the dire current trends in reef ecosystem health, combined with the scale at which intervention has to occur, are the greatest challenge to overcome for reef restoration approaches to succeed. To achieve scale, novel engineering solutions need to be developed alongside the urgent need to fill the critical research knowledge gaps for each proposed intervention and restoration strategy. Some approaches are achievable at the experimental scale (algal symbiont manipulation, shading) or with individual colonies in field settings (antibiotic treatment), but developing the technologies to allow delivery at the reef and ecosystem scales will require considerable investment in human and infrastructure capital.

Improved coordination among federal and nonfederal entities and across jurisdictional boundaries is important for addressing the long-term research needs. The recent establishment of the coral bleaching research coordination network (RCN) is one such attempt to accelerate efforts to understand coral bleaching by bringing research across interdisciplinary backgrounds together and standardize sampling and experimental protocols. This effort promotes the sharing and use of the highest value data by the community for management or other decisions. While the coral bleaching RCN is primarily focused on sampling, experimental, and data assimilation protocols, extending efforts to globally coordinate bleaching observations and establish a consistent monitoring framework for thermal stress tolerance and bleaching susceptibility across coral species would be highly valuable. Development of stable, long-lived databases and high-

performance computing resources that house such coral reef data would support analyses focused on resilience and restoration. The Coral Trait Database is a good example of a valuable resource that consolidates information pertaining to coral life history, phylogenetic, and biogeographic data; it is freely available to scientists and reef managers throughout the world (Madin et al., 2016). Expanding to coordinate bleaching observations, monitoring frameworks, and thermal stress thresholds, guided by an international program, would ensure these goals are reached. Such an effort would benefit from the leadership of core partner federal and international agencies, which together could serve as the primary entity for coordination of research nationally and internationally and for information dissemination.

Research and development activities can be streamlined through ensuring open access of data and information and facilitated through creation of coordinated and integrated databases. Such integration of data has been captured in existing collaborative projects such as the eReefs platform (https://ereefs.org.au) that incorporates a vast array of water quality, remote sensing, and hydrodynamic modeling to allow predictive forecasting of environmental parameters across the Great Barrier Reef. Building a similar resource for the Caribbean region would be highly valuable. Databases of management programs and relevant scientific studies (e.g., Conservation Evidence, https://www.conservationevidence.com) can facilitate knowledge transfer, development of best practices, and meta-analyses that quantify larger-scale outcomes and resolve context-dependences. Similarly, databases that report bleaching events, such as ReefBase, can significantly enhance understanding of ecosystem responses to changing environments and inform management actions. Development of standardized protocols and open data dissemination allows rapid assessment of the strength or weakness of datasets.

Training of a workforce that is highly skilled across the range of disciplines from field ecology, to engineering, to laboratory research and bioinformatics will facilitate the generation and dissemination of knowledge to a wide international audience. This workforce will need to include local, culturally-connected scientists, managers, and practitioners. Workforce and infrastructure capacity are important to develop within coral reef jurisdictions around the world. These far-reaching communities would need to be connected through well-developed outreach and communications that share scientific information and serve as a bridge to management and policy decisions.

6
The Tropical Western Atlantic and Caribbean as a Case Study for Coral Interventions

The committee was tasked with assessing coral intervention strategies and their ability to meet objectives for sustaining coral reefs in the tropical western Atlantic (which includes the Caribbean and neighboring reefs in the Gulf of Mexico and outlying reefs in the NW and SW Atlantic, such as Bermuda, Bahamas, and Brazil). These reefs vary widely in their condition and in the intensity of local stressors, and include areas that have experienced devastating coral reef losses in recent history. These losses have been due to the combined effects of a variety of factors, including disease outbreaks, bleaching events, and hurricane impacts, exacerbated by a variety of local stressors to which the reefs have had generally limited resilience.

Tailoring a decision strategy to a local area is a vital component of the decision process. In this chapter, the committee synthesizes the information about selecting and modeling interventions from the preceding chapters as it applies to the tropical western Atlantic and Caribbean. Specifically, which interventions may be particularly appropriate for consideration in this region given their context-dependencies is explored (as discussed in Chapter 2). How the impacts of these interventions would be assessed in a model tailored to particular environments in this region is also considered (Chapters 3 and 4). However, environmental context is only one component of a decision framework applied to a particular region; consultation with local stakeholders is also a necessary step in clarifying management objectives and identifying appropriate interventions (see Chapter 3). Because both stakeholder involvement and details of the local reef ecosystem dynamics are needed to inform and refine model development, and because the region varies considerably in these respects, it is beyond the purview of the committee to conduct a formal assessment of objectives, alternatives, and intervention plans for the region as a whole. As an initial, framing contribution, this chapter lays out the unique nature of the reef ecosystems in this region that form the basis for undertaking this process, and outlines opportunities for pursuing some of the priority research described in Chapter 5.

TROPICAL WESTERN ATLANTIC AND CARIBBEAN REEF ECOSYSTEMS: GEOGRAPHY, DIVERSITY, ECOLOGY, AND RESILIENCE

The tropical western Atlantic and Caribbean region, including the Caribbean Sea, Gulf of Mexico, Florida, Bahamas, Turks and Caicos, Bermuda, and Brazil (hereafter referred to as ‘the wider Caribbean’) is an important reef area globally. Although these reefs represent only ~8% of the world’s total reef area (less than half that of Indonesia or Australia; Spalding et al., 2001), they are of considerable biological, ecological, cultural, and socioeconomic importance. There are 23 countries and 18 overseas colonies and territories in the region that have coral reef resources. These areas range from the poorest nation in the hemisphere (Haiti) to areas that remain politically affiliated with major western economies, such as Puerto Rico and the U.S. Virgin Islands (United States); Anguilla, Antigua and Barbuda, the Bahamas, Barbados,

Bermuda, the Cayman Islands, Dominica, Grenada, Jamaica, Turks and Caicos, Montserrat, St. Kitts and Nevis, and the British Virgin Islands (United Kingdom); Guadeloupe, Martinique, St. Bart's, and St. Martin (France), and Aruba, Bonaire, Curacao, Saba, St. Maarten, and St. Eustatius (The Netherlands).

As a region, the wider Caribbean is oceanographically distinct. The Caribbean and Gulf of Mexico represent a comparatively small and semi-enclosed region, influenced by nutrients from the outflows of the Amazon, Orinoco, and Mississippi river basins, as well as by iron from wind-blown dust (Pawlik et al., 2016; Roff and Mumby, 2012; Shinn et al., 2000). This means that, even on arid Caribbean islands, terrestrial influences tend to be higher than they are in the more oceanic parts of the Pacific and Indian Oceans, with concomitantly higher nutrient loads, and larger algal and microbial biomass. Hurricanes are common in the eastern and northern Caribbean, but are nearly absent from the southern Caribbean (Chollett et al., 2012a). Moreover, the southern Caribbean and Bermuda are potential refugia for climate change (Chollett et al., 2010), having experienced less frequent and less severe bleaching events and tending to show longer times to annual severe bleaching (van Hooidonk et al., 2016).

The wider Caribbean has been completely isolated evolutionarily from the Pacific since the closure of the Isthmus of Panama about 2.8 million years ago (O'Dea et al., 2016), with periods of origination and extinction over the past 33 million years leading to its current distinctive and relatively low-diversity coral fauna (Budd, 2000). Today, the Caribbean and Pacific coral faunas are not closely related, with just a few shared genera (*Siderastrea*, *Porites*, and *Acropora*); notably, recent extinctions during the Plio-Pleistocene resulted in the loss of both *Pocillopora* and *Stylophora* from Caribbean reefs (Budd, 2000; Toth et al., 2015). Indeed, it is now recognized that, in a number of cases, Caribbean and Pacific scleractinian taxa that were originally thought to be congeners are actually in different families (Fukami et al., 2004), and some coral families are entirely or mostly restricted to the Caribbean (Fukami et al., 2008), with further endemism also characterizing Brazilian reefs. The characteristic algal symbionts associated with scleractinian corals also differ between the two reef regions (Baker and Rowan, 1997; LaJeunesse et al., 2003, 2018). Most corals in the Indo-Pacific host members of the genera *Cladocopium* and/or *Durusdinium*, whereas Caribbean corals commonly host *Symbiodinium*, *Breviolum*, *Cladocopium*, and/or *Durusdinium*. The latter symbiont genus may have been introduced from the Pacific (Pettay et al., 2015).

At the species level, reefs in the tropical western Atlantic are far less diverse than their analogs in the western Pacific; for example, there are only two species of *Acropora* (plus one hybrid) in the Caribbean, whereas there are hundreds in the western Pacific (Wallace, 2012). Similar diversity differences exist for reef fishes and other reef associates (Roberts et al., 2002). For this reason, it has been argued that Caribbean reefs lack the ecological/functional redundancy found on most Indo-Pacific reefs (Bellwood et al., 2004; McWilliam et al., 2018; Roff and Mumby, 2012). Nevertheless, until relatively recently (the 1970s), percent coral cover was similar on reefs in the Caribbean and the Indo-Pacific, with reefs in both areas commonly reaching or exceeding 50% coral cover (Bruno and Selig, 2007; Gardner et al., 2013; Jackson et al., 2014). However, ecological decline of Caribbean reefs accelerated greatly beginning in the late 1970s, resulting in changes far greater than any observed during the previous 220,000 years (Jackson, 1997; Pandolfi and Jackson, 2006).

Basin-wide, major disease epizootics have been responsible for triggering some of the greatest changes. These began with the die-offs of structurally dominant elkhorn and staghorn corals (*Acropora palmata* and *A. cervicornis*) in the late 1970s (Aronson and Precht, 2001; Gladfelter, 1982) followed by the loss of a keystone herbivore, the black-spined sea urchin (*Diadema antillarum*) in the early 1980s (Lessios, 1988). Declines in herbivory altered the competitive balance between fast-growing algae and slow-growing corals in a way that is now recognized as a fundamental property of coral reef ecosystems around the world (see Figure 6.1; Hughes, 1994). In some cases, corals have been replaced by other organisms such as octocorals or sponges (Norström et al., 2009; Ruzicka et al., 2013).

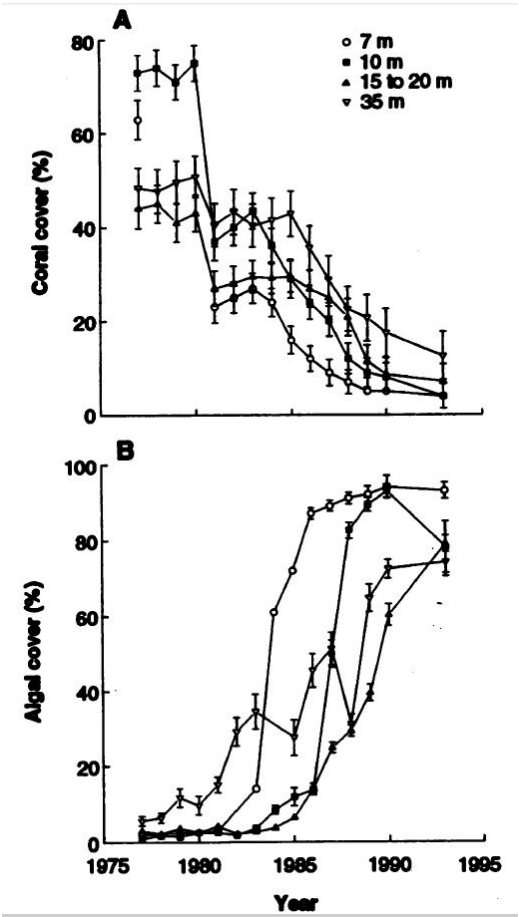


Figure 6.1 Figure showing the reciprocal change in (A) coral cover and (B) algae on Jamaican reefs after the die off of the sea urchin *Diadema antillarum.* SOURCE: Hughes, 1994

Other diseases have also directly impacted coral populations (e.g., yellow band disease, black band disease, and various white syndromes), including the recent emergence of Stony Coral Tissue Loss Disease (SCTLD), described below. It is possible that the wider Caribbean may be particularly vulnerable to disease due to its long isolation (Bak et al., 1984). Pathogenic agents are varied and remain generally unknown or uncertain (including some of the most important, such as the pathogen that decimated *D. antillarum*). Nevertheless, it is likely that anthropogenic impacts (e.g., nutrient pollution, algal overgrowth, and warming) have played a role in the rise of these diseases as ecological drivers (Lesser et al., 2007).

Diseases have not been the sole driver of coral decline in the region. Overfishing has compounded the impacts of the loss of *D. antillarum* (Hughes, 1994; Jackson et al., 2014), and the invasive lionfish, which has recently spread rapidly through the region, has aggravated the impacts of overfishing by preying on juvenile fish (Côté et al., 2013; Eckrich and Engel, 2013; Willette et al., 2014). Nutrient levels as well as differences in the diversity and abundance of fish herbivores, in particular, could help explain the apparent vulnerability of reefs in the wider Caribbean to algal overgrowth. Poor land-use practices (Bégin et al., 2013) and storm-driven wave surge (Knowlton, 2001) have also contributed to coral mortality by increasing sedimentation, nutrients, and turbidity. These sources of damage have in some cases led to the physical flattening of Caribbean reefs, i.e., loss of three-dimensional structure, especially in shallow forereef and reef crest communities (Alvarez-Filip et al., 2009; Knowlton, 2001).

Taken together, these events and processes have had major impacts on Caribbean coral reef structure. Variation in these impacts, some local, some regional, some global, have led to marked heterogeneity in degradation among Caribbean reefs (Jackson et al., 2014; Knowlton and Jackson, 2008). At the same time, there has been widespread recruitment failure in some areas of the wider Caribbean, such as Florida, while recruitment has remained relatively high in other locations, such as Curaçao (Hartmann et al., 2018). Consequently, the trajectory of coral decline has not been uniform, and some areas have retained markedly higher coral cover than others (Jackson et al., 2014).

This suggests that the basic ecosystem dynamics of competition between fast-growing algae and slow-growing corals remains a powerful controlling force set by herbivory and growth rates, that local reef impacts due to fishing, land use, and tourism are common, and that local management still has an important role to play in potentially slowing or even reversing Caribbean degradation (McLeod et al., 2019), even if these effects can be hard to detect (Bruno et al., 2019; Steneck et al., 2018).

Across this mosaic of local and regional effects, climate change impacts are increasing, and in the wider Caribbean, as elsewhere, there are limits to the effectiveness of local management. The western Atlantic has experienced background warming of about 0.015°C yr^{-1} on average (Glenn et al., 2015), but also shows substantial variability in rates of warming (Chollett et al., 2012b). This warming affects corals directly, via heat-driven coral bleaching (Donner et al., 2007; Eakin et al., 2010), and indirectly by increasing intensities of tropical storms (Bhatia et al., 2019; Murakami et al., 2018) and more devastating coral disease epizootics (Harvell et al., 1999). For example, the 2005 warming event that affected the northeastern Caribbean caused over 10.2 degree heating weeks of thermal stress that resulted in more than 80% of corals bleaching and more than 40% of corals dying at many sites (Eakin et al., 2010). Bleaching was then followed by severe disease impacts (Miller et al., 2009; T. Smith et al., 2013). Severe bleaching was also observed in 2010 in some parts of the Caribbean (Alemu and Clement, 2014; T. Smith et al., 2013), also followed by disease outbreaks. Repetitive bleaching in Florida in 2014 and 2015 was also accompanied by disease (Gintert et al., 2018; Precht et al., 2016), as described below.

Recent Emergence of a Highly Lethal Coral Disease

Recently, a new disease syndrome, Stony Coral Tissue Loss Disease (SCTLD), has emerged in Florida and parts of the central and northeastern Caribbean. The disease is an extremely virulent and persistent epizootic affecting a large proportion of coral species and consequently threatening coral diversity. This disease accompanied repetitive bleaching in Florida in 2014 and 2015, and is illustrative of the problem of compounding threats to coral persistence. It also serves as a reminder of how disease presence within coral populations might change how some interventions, such as those designed to increase thermal tolerance, might be implemented.

SCTLD was first documented in 2014 by contractors monitoring the environmental impacts of dredging at the Port of Miami at the northern end of the Florida Keys (Precht et al., 2016), and has since spread both north and south, reaching the northern limit for reef-building coral off Martin County, Florida by 2017 and extending south to Looe Key (near Key West) by early 2018 (NOAA, 2019). As of May 2019, SCTLD had reached Sand Key, about 5 miles southwest of Key West (Florida DEP, 2019). SCTLD affects up to 22 species, but with significant variation among them in the severity and extent of the disease. Rates of mortality are high in susceptible species, and can reach 100%, resulting in locally severe impacts on species diversity and potentially widespread reductions in genotypic diversity. The outbreak has prompted an interagency rescue effort—the Florida Reef Tract Rescue Project—to collect genotypes from ahead of the disease front and maintain them in ex situ land-based facilities until reintroduction and restoration can occur with a high chance of success. The causative agent (or agents) is not known, but waterborne transmission has been demonstrated. Disease lesions have been successfully treated with antibiotic pastes (Neely, 2018), suggesting a bacterial pathogen with potential co-relationships with viruses.

Unlike most diseases, which tend to flare up over the warmer summer season and then disappear over the cooler winter months, SCTLD has persisted and continued to spread over multiple years. The initial appearance of the disease followed a bleaching event in late 2014, but then spread to affect corals that had already recovered from bleaching. The subsequent spread of the disease does not appear to have been linked to continued thermal stress. By spring 2018, corals with disease signs similar to SCTLD were reported in Jamaica (AGRRA, 2018), and by July 2018, it was reported from Puerto Morelos, Mexico (Alvarez-Filip, 2018). The disease had spread to St. Maarten by November 2018 (The Daily Herald, 2018), the U.S. Virgin Islands by February 2019 (The Virgin Islands Consortium, 2019) and the Dominican Republic by March 2019 (Irazabal and Rodriguez, 2019). The relatively rapid and sudden appearance of the disease outside the Florida Reef Tract highlights the high interconnectivity of wider Caribbean reefs and the capacity for the rapid spread of diseases (which, with invasive species, is a risk factor for some interventions considered in this report), although the location of new outbreaks near ports may indicate transport by humans rather than via currents. There is concern that SCTLD, if it continues to spread regionally, has the ability to transform wider Caribbean reefs, as previously happened following the epizootic that decimated *Diadema* in 1983-84, and the loss of *Acropora* from White Band Disease in the 1970s and 1980s. In affected areas, such as Florida, it is not known if the disease will abate once susceptible individuals are removed from the population, or if the disease will remain a chronic problem once the initial outbreak has passed through.

IMPLICATIONS FOR SELECTING AND MODELING INTERVENTIONS

The environmental context of the wider Caribbean has direct implications for how to approach the decision to implement coral interventions. Here, the committee identifies the context dependencies that would influence analyses aimed at deciding which interventions to test and deploy (as discussed in Chapters 2, 3, and 4), as well as the environmental parameters that would be important to include in a dynamic coral model where the risks and benefits of the intervention(s) may be evaluated.

Generally poor conditions and intrinsic vulnerability: In general, the Caribbean appears to have low resilience (a resilience "coolspot"; Roff and Mumby, 2012) with less functional redundancy in the wider Caribbean compared to the Indo-West Pacific (McWilliam et al., 2018) and characteristics that promote algal overgrowth of corals. The wider Caribbean is generally further along the trajectory of decline than the Pacific (Gardner et al., 2003; Jackson et al., 2014; Roff and Mumby, 2012), although degradation of reefs in some areas of the Pacific is increasing (Bruno and Selig, 2007; De'ath et al., 2012; Hughes et al., 2018). As noted above, some wider Caribbean reefs have low coral cover, rampant disease, lack rapidly growing branching corals, and show very low coral recruitment. These attributes may imply potentially higher risk tolerance for interventions for some reef managers in these particularly degraded areas (e.g., Florida). On the other hand, lower resilience and poor condition may mean a higher risk of crossing a harmful tipping point or a lower likelihood of success when interventions are applied.

Generally poor conditions on such reefs demand models of interventions (e.g., as illustrated in Chapter 4) that include starting scenarios of low coral cover, poor recruitment and vigorous algal growth. Additionally, processes representing local stressors, such as overfishing (which reduces herbivory) and poor water quality (which can accelerate disease and algal growth), will be important to evaluate to consider the impact of their management in comparison to the impact of, or need for, coral interventions. Reef models that evaluate interventions need to be parameterized with initial conditions that reflect current conditions of reefs in the wider Caribbean, including regional variability in reef ecosystem health, impacts of stressors, and community attitudes on risk acceptance.

Interconnectedness: The rapid spread of diseases and invasive species indicates that both the risks and benefits of biological interventions could spread quickly in the wider Caribbean. On the one hand, this suggests that there are relatively few isolated reefs that might be safe spots to test risky interventions in the field (see Chapter 2). But, on the other hand, local increase and spread of heat tolerant genotypes, disease-resistant colonies, or heat resistant symbionts might lead to regional benefits. It may be, for example, that the heat resistant symbiont *Durusdinium trenchii* has already invaded the Caribbean from the Pacific (as opposed to being native; Pettay et al., 2015). For interventions that realize both benefits (through enhanced connectivity) and risks (through disease spread), such as assisted gene flow and assisted migration, incorporating this interconnectedness into a modeling framework can reveal whether interventions can outperform expectations from natural dispersal and assess the spatial scale of risks.

Differences in diversity of coral and algal symbionts: Algal symbiont diversity at the generic level is high in the Caribbean compared to the Indo-west Pacific (IWP), but total species

diversity (of both coral hosts and algal symbionts) is lower. The implications are uncertain: lower diversity could mean either greater or lower responsiveness to interventions. Disentangling the role of diversity on multiple levels, including the relative efficacy of interventions to promote different types of diversity, would require a multispecies or genetic modeling framework of coupled host-symbiont dynamics.

Environmental variability: The fact that Bermuda and the southern Caribbean may represent climate refugia, with long periods of time between bleaching events (van Hooidonk et al., 2016), has implications for the geography of interventions. These areas may have sites where protection of existing biodiversity is central to a suite of interventions, although these sites may also be less likely to contain genotypes of corals or symbionts that are highly heat resistant. Conversely, areas like the Florida Keys, where reefs are already relatively highly degraded, may find more risky interventions to be acceptable in order to provide outcomes that enhance reef persistence. Making distinctions between different areas within the larger Caribbean region would require models with location-specific parameterizations including downscaled climate models and local stakeholder and management input.

Ongoing acute disease outbreak: The presence of diseases, such as SCTLD, has the potential to change the way that thermal stress interventions are applied on Caribbean reefs, and provides a sobering lesson on the complexities of implementing interventions in the face of multiple stressors. Some interventions, such as pre-exposure, are likely to be much less effective during a disease outbreak because the application of an additional stressor to a diseased coral may be more likely to lead to mortality. In addition, bringing diseased corals into a laboratory setting and then re-deploying them in the field may set the stage for laboratory-based transmission. Other interventions, such as managed relocation, may have extremely adverse effects if undertaken during a disease outbreak, for example if corals are moved from an area where the disease is endemic to an area where the disease is not present. These interventions might well be rejected in such a case. Even moving corals in the opposite direction—from outside the diseased area into the diseased area—could exacerbate the disease by increasing the number of susceptible corals and fueling the spread of the disease in the endemic area.

Diseases such as SCTLD, by greatly reducing population size, also threaten to decrease the pool of potentially heat-resistant alleles available for genetic interventions designed to promote the spread of those alleles. As a result of this concern, efforts are already underway to safeguard coral diversity in areas not yet exposed to SCTLD by removing representatives of susceptible species from reefs and holding them in ex situ facilities, until such time as they can be used in a subsequent restoration program or applied to another conservation purpose. If the disease becomes chronic, continuously impacting susceptible species, these ‘rescued’ corals may not be suitable for restoration inside the endemic area, and indeed corals sourced from inside these endemic areas may not be able to be used for restoration outside the same area. Such impacts underscore the need to prospect for coral genotypes that are both heat-resistant and disease-resistant (e.g., Muller et al., 2018), and to understand the genetic underpinnings of both as a part of a comprehensive intervention strategy, an ambitious goal. Interventions that focus on the treatment of disease (e.g., antibiotics, phage therapy, and microbiome manipulation) are clearly warranted in response to SCTLD, and testing such interventions is now a priority on affected reefs. A modeling framework that explicitly incorporates strong disease dynamics as they relate

to both risks (disease spread for interventions that entail moving corals) and benefits (interventions that might enhance disease resistance) is particularly relevant to the wider Caribbean.

Finally, the rapid and extreme impacts of SCTLD in Florida—a relatively degraded coral reef system—may change managers' risk tolerance and willingness to attempt interventions. The perceived risk of interventions may be considerably lower than the risks of disease-driven reef declines. The coral disease responses currently being executed in Florida includes some activities that are starting points for coral interventions, such as the relocation of corals from outside the disease endemic zone to ex situ land-based facilities to preserve genetic diversity in advance of the disease spreading. Responses are now being considered that would have faced higher resistance until very recently, such as removals of infected colonies to reduce pathogen loading (currently being attempted in the U.S. Virgin Islands; Marilyn Brandt, personal communication).

Small but politically complex region: Many countries effectively share coral reef resources and will also share risks and benefits of interventions. Some outliers, notably Bermuda and Brazil, are isolated from other reef systems (or at least represent the end points in a connectivity network), and thus may have the ability to pursue interventions more unilaterally. Several Caribbean possessions or territories are still governed by former colonial powers (the United States, the United Kingdom, France, and the Netherlands), and these nations have jurisdictions that cover fairly broad and discontinuous areas. However, many other reef regions within the Caribbean (e.g., the Lesser Antilles) are managed by multiple countries.

Some interventions, such as cloud brightening to reduce surface water temperature, or assisted gene flow over hundreds of miles, operate on a large enough scale to demand regional coordination. Other interventions, such as larval seeding or assisted gene flow over small distances, may be able to be accomplished within a very small jurisdiction. In the wider Caribbean, the degree of coordination between countries will affect the feasibility of using those interventions that necessarily cross borders (i.e., those that move corals from one area to another, or those that are likely to spread outside their direct area of implementation).

OPPORTUNITIES FOR INTERVENTIONS

The committee was tasked with assessing the interventions in expected near-future environmental conditions in the Caribbean region, relative to objectives and performance measures for conserving coral reefs. Selection of management objectives and associated metrics (e.g., Table 3.1) is a stakeholder-driven process that also includes an assessment of acceptable courses of action to meet these objectives (described in Chapter 3) that the committee did not undertake. The committee does not recommend specific objectives, and did not systematically review the applicability of all possible interventions for the Caribbean region, which are outlined in detail in the previous report (NASEM, 2019). Instead, the committee highlights interventions that stand out as being particularly well-suited to the region, given the considerations of ecology, history, current state, and existing capacity outlined above. They therefore reflect the regional context and the context dependencies of the interventions, and reflect the assessments of Chapter

2. Depending on community objectives, these strategies, alone or in combination across different sites throughout the region, would be considered within a structured decision framework.

It should also be emphasized that these interventions are not intended as a substitute for conventional management actions, which continue to be essential across the Caribbean, with particular attention being paid to maintaining water quality and herbivory in local management jurisdictions. The importance of this point is supported by the fact that much of the decline of Caribbean reefs occurred prior to the onset of major bleaching events (Gardner et al., 2003), and also by the preliminary modeling results presented in Chapter 4. Similarly, these interventions cannot be expected to conserve coral reefs in the absence of actions to reduce climate change impacts such as through emissions reductions and carbon sequestration.

All interventions would benefit from additional research to improve their efficacy and understanding about their risks and benefits. Chapter 2 includes an assessment of which interventions are closest to being technically ready for implementation in the near-term, were they to be identified as favorable options through a structured decision process. Ultimately, research is likely to be needed to understand and improve the efficacy of many other interventions in the Caribbean, and undertaking this decision process can help identify research priorities to improve promising interventions not ready for implementation. Some research needs are also mentioned here, to highlight priority research relevant to the Caribbean more thoroughly explored in Chapter 5.

Identifying heat tolerant or disease resistant coral genotypes among the Caribbean standing stock to provide opportunities for assisted gene flow, managed breeding, and genetic interventions: Understanding the intraspecific range of thermotolerance would be helped by obtaining a better understanding of population structure of Caribbean species among habitats, localities, and regions. Moreover, quantitative data on the environmental differences among habitats would help with the interpretation of these data. Many species have habitat-specific subpopulations and, while not unique to the Caribbean, the restricted fauna offers an opportunity to fully understand key reef-building species and their potential range of thermal responses. In addition, a broad diversity of habitats and a historically species-poor fauna may have allowed significant habitat specialization within species. If so, this could be harnessed in interventions.

Some individuals of important reef-building Caribbean taxa (e.g., *Orbicella* and *Acropora*) have shown resistance to thermal stress, disease, and reduced water quality in the lab (Muller et al., 2018) and field (large colonies with low partial mortality after disturbance). Research into the basis of this resistance and co-resistance could identify alleles for use in propagation and managed breeding. More immediately, large scale ongoing efforts to outplant corals could include monitoring of heat, disease and water quality resistance among the varied suite of nursery colonies across these varied efforts. Because research has shown that colonies with different genotypes and symbionts can differ strongly in these traits (see Muller et al., 2018 for a Caribbean example), systems for tracking coral/symbiont genotypes in nursery settings are being developed (Kitchen et al., 2018). Similarly, identification of algal symbionts or microbiome components that confer resilience to stress would help restoration practitioners select resilient corals, or provide insight into how to manipulate holobionts in favor of resilient types (Cunning et al., 2018; Silverstein et al., 2015). A system of best practices for coral restoration that

leverages these efforts to provide information on resistant colonies would parallel similar long-standing efforts in terrestrial restoration and agriculture.

Leveraging existing coral restoration activities and infrastructure to create a comprehensive region-wide program to boost larval recruitment and survivorship: Given that the ultimate goal of asexual restoration is to produce sexually reproducing, self-sustaining populations that can maintain genetic diversity and therefore potentially be more hardy in future conditions, more effort could be invested in determining the extent to which this is actually occurring in ongoing restoration programs. Restoration practitioners could be encouraged and incentivized to quantify the frequency, incidence, and output of sexual reproduction among outplanted corals, determine the biotic and abiotic parameters that are associated with sexual maturity and fecundity, and modify outplanting protocols to maximize eventual sexual reproduction. This leverages existing infrastructure and represents an opportunity to build supportive breeding activities into ongoing asexual restoration programs that are currently focused on outplanting, greatly increasing the long-term impact of these activities. Rather than representing an additional burden on restoration practitioners, incorporating breeding programs into nursery and outplanting activities could be encouraged and incentivized by funding agencies as part of scaling up. In addition to the value of producing coral recruits, sexual reproduction among colonies with diverse combinations of alleles can maximize opportunities to produce successful genotypes. This would be potentially advantageous for two objectives: (1) resisting impacts from climate change, but also (2) preserving diverse assemblages more capable of resisting the multiple stresses experienced in the most degraded Caribbean reefs.

A limiting factor in the success of these efforts is the relatively low natural levels of sexual reproduction and coral recruitment in some areas of the wider Caribbean region that might severely limit the success of managed breeding programs. While progress is being made in developing interventions in some areas of the Caribbean that have high recruitment (e.g., in Curaçao; Hartmann et al., 2018), it is not known whether low success in other areas is a result of intrinsic factors that might in theory be resolved by interventions and restoration (e.g., low genetic diversity and inbreeding) or is driven by extrinsic environmental factors that cannot be directly improved by interventions considered here and is better managed through standard management actions (e.g., improving water quality or increasing herbivory).

Exploiting sexual restoration activities to test algal symbiont manipulations: Existing programs to collect, settle, and outplant coral larvae could also incorporate algal symbiont manipulations to test whether coral recruits can be supplied with different algal symbiont types, in particular thermotolerant *Durusdinium trenchii* (Williamson et al., 2018). Such trials could also determine whether these symbionts are retained into adulthood and increase heat tolerance, and be used to assess potential tradeoffs, such as reduced growth rates (Little et al., 2004).

Expanding coral cryopreservation across the region to provide opportunities for managed breeding and assisted gene flow: Dissemination and training in protocols for gamete cryopreservation (e.g., Hagedorn et al., 2012, 2017) would allow researchers and restoration practitioners working on coral spawning to preserve gametes, both for long-term gene banking purposes to guard against continued loss of diversity, and for immediate use in managed breeding and assisted gene flow (Hagedorn et al., 2018) programs, where, by necessity, either

sperm or eggs must be frozen and transported for later use in fertilization trials. Space could be acquired in existing national gene bank facilities to preserve these genetic materials long-term.

Testing short-distance managed relocation (i.e., assisted gene flow) of corals across local thermal gradients, where disease incidence is not a limiting factor: Efforts could be made to prioritize projects with the potential to increase heat tolerance by sourcing resistant corals within management jurisdictions, across minimal relocation distances (Baker et al., 2018). Areas could be identified that are already under elevated thermal regimes, with adapted/acclimatized corals being used as source populations. Identifying locations where naturally occurring heat- or disease-resistant corals are more common might help efforts to provide raw material for nursery propagation and/or managed breeding, as above.

Extending relocations over larger distances would require balancing the potential gains in thermal tolerance (that exist due to large variation in thermal tolerance across the region), with the potential loss of fitness due to local selection (which may have already tuned adult corals to the particular physical environmental conditions at their respective natal sites), as well as the risks associated with spreading disease highlighted above. Testing whether heat tolerant corals sourced from distant locations can survive equally well as their local counterparts under non-bleaching conditions remains an open question, not just for the Caribbean, but for translocations in other regions as well.

Leveraging restoration activities to test pre-exposure methods to increase stress tolerance of outplanted corals: Existing restoration activities in the region provide an opportunity to test pre-exposure interventions designed to increase thermal tolerance. For example, acute methods of pre-exposure, such as controlled bleaching and recovery of corals prior to outplanting, may increase the abundance of heat tolerant *Durusdinium trenchii* (Cunning et al., 2018), and pilot tests are determining the feasibility of this intervention, as well as assess the longevity of its impacts and potential tradeoffs (Cabral et al., 2018; Winter et al., 2018). Similarly, testing whether chronic "stress-hardening" nurseries located at sites with more disturbed conditions can generate stocks of hardy corals for outplanting through pre-exposure might also be worthwhile. Such approaches can increase heat tolerance by promoting different algal symbionts (or microbiome communities), as well as other potential effects, such as front-loading of coral heat tolerance genes (Barshis et al., 2013).

Assessing feasibility of environmental interventions to reduce heat stress at both local and subregional scales: Shading and cooling interventions may reduce the degree of thermal stress, and atmospheric shading may do so in a way that operates at large scales. Although early modeling suggests that the marine cloud layer is less suitable for cloud brightening in the Caribbean (Alterskjær et al., 2011), it would be important to determine if this applies to the warm season when bleaching conditions (doldrums) occur. Monitoring the growing risk from ocean acidification would also inform interest in implementing ocean acidification interventions.

Testing interventions, such as antibiotics, phage therapy, and microbiome manipulations, to halt the spread of emerging diseases, improve coral condition, and increase the success and/or feasibility of other interventions: The relatively high vulnerability of the Caribbean to disease, and the current spread of panzootics such as SCTLD, mean that this region is a high priority for

testing and implementing disease interventions. There is a clear need to investigate techniques to slow, block, and halt the disease (such as antibiotics, phage therapy, and microbiome manipulations/probiotics) as well as approaches to preserve genetic resources prior to the arrival of a nearby disease front. There is an urgent need to develop quarantine and disinfection procedures to minimize the unintended spread of these interventions beyond the immediate site of interest. Active diseases in these areas also affect other interventions unrelated to disease that might introduce or spread pathogens (e.g., managed relocation). As discussed above for SCTLD, some interventions, e.g. pre-exposure or managed relocation, may be counter-productive if undertaken during an active disease outbreak.

Combining interventions where possible to increase resource efficiencies: As noted in Chapter 2, combined efforts can promote efficiency and could be profitably explored. For example, a sexual restoration program described above could incorporate both symbiont manipulations of larvae and cryopreservation of gametes, used to assess the heritability of resistant traits such as disease resistance, or to cross disease resistant genotypes with a native population in order to boost disease resistance.

Testing the efficacy of interventions under a range of different conditions by exploiting variability in the degree of degradation across the region: Areas of the wider Caribbean that are relatively intact (e.g., Curaçao, Bonaire, and Bermuda), could be compared with areas that are relatively more degraded (e.g., the Florida Keys) to test if the outcomes of interventions vary as a result of initial conditions, both for comparative modeling and for field testing. In addition, this same concept could also be applied within these areas where heterogeneity in reef degradation exists over local scales. It would be useful to know if certain areas of the Caribbean (e.g., the Florida Keys) are already unsuitable for interventions because underlying conditions from other stressors, apart from thermal stress, are already inimical to coral reefs.

More generally, resistance of Caribbean corals to thermal stress can be high in some cases (T. Smith et al., 2013), yet recovery, the other component of resilience, can often remain very low (Roff and Mumby, 2012; Jackson et al., 2014). This is fundamental to understanding the long-term trajectory of Caribbean corals and the benefit of interventions. Resilience science—understanding factors that promote or inhibit recovery from disturbance—is critical in the Caribbean and is central to understanding if interventions will have long-term success. For example, it is still an open question whether dust from the Sahara negatively impacts Caribbean resilience (Shinn et al., 2000), yet this could be fundamental to understanding the impact of interventions. In addition, interventions that promote recovery by breaking positive feedbacks cycles (e.g., restoration of genetically diverse stands of *Acropora cervicornis*; Roff and Mumby, 2012) could be identified.

Developing regional and multinational coordination and agreements to meet the scale of the challenge: The large number of jurisdictions in the Caribbean suggests it may be beneficial if a program to manage and coordinate intervention efforts regionally were established and supported, perhaps as a working group of the Coral Restoration Consortium (http://www.reefresilience.org/restoration/coral-restoration-consortium/). Some of these efforts have already begun, for example the multi-institution Florida Reef Tract Rescue Project currently ongoing for SCTLD within Florida (Florida DEP, 2019). These coordinated efforts

could help share successes and avoid waste on duplicative failures, although not at the expense of innovation and risk-taking. Internationally, large-scale cooperative research and funding agreements could be pursued, both through international agencies (e.g., World Bank, United Nations Environment Programme) and intergovernmental collaborations (e.g., a U.S.-Australia binational agreement).

Soliciting and incorporating stakeholder input on interventions to gauge and maximize acceptability/social license: Dramatic differences in reef health and economic resources across the region, as well as the multinational, multilingual, and multicultural nature of the Caribbean region, mean that assessments of intervention feasibility are likely to be variable across these gradients and will change with time.

Conclusion: Coral reef managers in the tropical western Atlantic/Caribbean region have a variety of interventions available to them depending on the localized management context and the specific objectives of stakeholders and decision makers. Available actions include leveraging existing restoration and propagation infrastructure, increasing sexual reproduction and genetic diversity of corals (managed breeding, gamete and larval capture and seeding, coral cryopreservation), capitalizing on thermally tolerant species and genotypes (managed selection, algal symbiont manipulation), accelerating reef connectivity to boost thermal tolerance when disease is not a factor (managed relocation), reducing disease spread (antibiotics, phage therapy, microbiome manipulation), and/or reducing exposure to stress (environmental interventions). The complex disease geography in the Caribbean requires particular care to ensure that interventions do not facilitate the spread or severity of ongoing disease outbreaks. These rapidly developing new interventions do not replace the need for direct management of local stressors.

Recommendation: The ongoing management and restoration efforts in the Caribbean provide a strong foundation on which to implement newly emerging interventions designed to increase the resilience of individual corals and coral populations. The modeling and decision-making tools outlined in this report should be used to inform more detailed assessments to evaluate which approaches might be appropriate for specific settings, including their interactions with more traditional management approaches. Maintaining genetic diversity in the face of multiple climate-driven stresses (e.g., bleaching and disease) is particularly important. Monitoring corals to maintain genetic diversity and identify resistant phenotypes should be simplified and standardized for research, ex situ propagation, and in situ restoration. Research programs to model and field test the risks, benefits, and efficacy of interventions in this multinational and highly inter-connected region should be coordinated to maximize resources, co-learning opportunities, and the ability to achieve management objectives regionally.

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Appendix A
Committee and Staff Biographies

COMMITTEE

Stephen R. Palumbi serves as the Jane and Marshall Steel Professor in Marine Sciences and Senior Fellow with the Woods Institute for the Environment at Stanford University. He is the former director for Hopkins Marine Station at Stanford. His research interests include the use of molecular genetics techniques to study evolution and change within the marine populations. His laboratory is currently studying the adaptive potential of corals in response to climate change. Dr. Palumbi has contributed to enhancing understanding of speciation patterns in open ocean systems, providing insights for marine reserve design and refuges for thermally sensitive corals. Dr. Palumbi has been awarded the Peter Benchley Award for Excellence in Science and was elected a member of the National Academy of Sciences, Fellow of the California Academy of Sciences, and Pew Fellow in Marine Conservation. He has published three books focusing on science for the general public, co-founded the microdocumentary series Short Attention Span Science Theater, and appeared in numerous ocean documentaries. After receiving his BA in biology from John's Hopkins University, he attained his PhD in zoology from the University of Washington with a concentration in marine ecology.

Ken R. N. Anthony is a principal research scientist at the Australian Institute of Marine Science. He is also an adjunct professor for both the University of Queensland and Queensland University of Technology. His main research focus is currently in the development of tools to support coral reef conservation management strategies and effective decision-making through the use of decision science, risk modeling, and adaptive management. He works with diverse stakeholders and management agencies to design conservation strategies to build resilience in coral reefs. He received a BSc in biology and an MSc in marine biology from the University of Copenhagen, and a PhD in coral reef ecology from James Cook University.

Andrew C. Baker is an associate professor at the University of Miami's Rosenstiel School of Marine and Atmospheric Science. Dr. Baker's research focus is on the impacts of climate change on marine ecosystems, particularly the relationship between reef-building corals and their diverse algal symbionts to understand how corals adapt to warming ocean temperatures and increased acidification. His work involves the study of physiological and molecular ecology, conservation biology, and population genetics. Dr. Baker's laboratory currently studies coral bleaching and thermotolerance, the genetic connectivity of corals in the Florida reef tract, and the links between deep and shallow reefs. He has also performed experimental work investigating how inoculating corals with heat-tolerant algae may improve temperature resilience. In 2008, he was named a Pew Fellow in Marine Conservation for his work with coral reefs and their response to climate change. Dr. Baker received his undergraduate degree from Cambridge University in zoology and his PhD from the University of Miami in marine biology.

Marissa L. Baskett is an associate professor in the Department of Environmental Science and Policy at the University of California, Davis. Her research focuses on modeling ecological and

evolutionary responses to global environmental change, including understanding potential drivers of resilience in coral reefs. She is particularly interested in evaluating the impact of management options on populations, looking at gene flow and local adaptation, and has initiated a project focusing on the potential for managed relocation of species at risk to climate change. She was selected as an Ecological Society of America Early Career Fellow in 2013. She received her BS in biology from Stanford University and her MA and PhD in ecology and evolutionary biology from Princeton University.

Debashish Bhattacharya is a distinguished professor in the Department of Biochemistry and Microbiology at Rutgers University, New Brunswick. His research interests lie in the genomics and bioinformatics of algal evolution, symbiosis, and biodiversity. He has been working with collaborators to understand coral genome evolution, biomineralization, and interactions with symbionts. His honors include election as a fellow to the American Association for the Advancement of Science in 2007 and receipt of the Darbarker Prize from the Botanical Society of America in 2008. He received his BS in biology and master's in environmental studies from Dalhousie University and his PhD in biology from Simon Fraser University.

David G. Bourne holds a joint appointment as a principal research scientist at the Australian Institute of Marine Science and a senior lecturer in marine biology at James Cook University. His research interests are in microbial diversity and their structure and function in complex ecosystems, and in the past 15 years has focused on symbiotic microbial interactions with coral. He is engaged in research on the microbial communities associated with corals and their contributions toward coral fitness, and in studying pathogens and mechanisms of diseases in coral and the effects these stresses can have on the reef ecosystem resilience to climate change. Dr. Bourne received his bachelor's and doctorate degrees in biotechnology from the University of Queensland in Brisbane.

Nancy Knowlton is a coral reef biologist and the Sant Chair for Marine Science at the Smithsonian Institution and senior scientist emeritus at the Smithsonian Tropical Research Institute. Previously, she was a professor at the Scripps Institution of Oceanography at the University of California, San Diego and founder of the Scripps Center for Marine Biodiversity and Conservation. Her areas of expertise include marine biodiversity and conservation, and evolution, behavior, and systematics of coral reef organisms. Her revolutionary studies of reef bleaching and speciation provide fundamental insights into differentiation and mutualism. Her work has revealed new, unexpected levels of diversity in the marine microbial environment. She is a member of the National Academy of Sciences. In 2009 she was awarded the Peter Benchley Award for Science in Service of Conservation. She received a BA in biology from Harvard University and her PhD from the University of California, Berkeley, in zoology.

Cheryl A. Logan is an associate professor in the School of Natural Sciences at California State University, Monterey Bay. She studies the physiological mechanisms marine animals use to survive in their changing environment and how this leads to differential success across species. She is involved in ongoing work modeling corals' potential adaptive ability to respond to rising temperatures and ocean acidification based on IPCC future climate scenarios. She received her BA from the University of California, Berkeley, in molecular and cell biology and integrative biology, and she received her PhD in biology from Stanford University.

Kerry A. Naish is a professor in the School of Aquatic and Fishery Sciences and Director of Marine Biology at the University of Washington. Her research focus is on characterizing the genetic diversity and fitness of aquatic populations, and how examining how these populations respond to natural and anthropogenic influences. She has particularly been involved in efforts to understand the consequences of population enhancement on the fitness of salmon and trout, the ecology and evolution of hosts and pathogens in coupled natural and wild systems, and the development of proactive approaches to population recovery. She is an Associate Editor of the journal *Evolutionary Applications*. Dr. Naish received her BS from the University of Cape Town, her MS from Rhodes University, and her PhD from the University of Wales, Swansea.

Robert H. Richmond is the Director and a research professor at the Kewalo Marine Laboratory at the University of Hawaii at Manoa. He received his doctorate in 1983 from the State University of New York at Stony Brook with a concentration in biological sciences. His research interests are focused on coral reef ecosystems, with studies including coral reproductive biology, ecotoxicology, coral reef ecology, and the impacts of climate change. In 2006, he was awarded a Pew Fellowship in Marine Conservation during which he developed molecular biomarkers of stress in corals as a tool for coral reef conservation. In 2014, he received an award from the U.S. Coral Reef Task Force in recognition of advancing scientific research, mentoring, and service. He has been awarded a grant from the Hawaii State Department of Health to develop biomarkers of toxicant exposure in corals in Hawaii. Dr. Richmond is currently a member of the Palau International Coral Reef Center's Board of Directors, as well as a member of the Climate Change and Coral Reefs working group at the Center for Ocean Solutions. He is the past President of the International Society for Reef Studies and served as the convener for the 13th International Coral Reef Symposium held in Hawaii in 2016.

Tyler B. Smith is a research associate professor of marine biology at the Center for Marine and Environmental Studies at the University of the Virgin Islands. His research interests include coral reef refuges and refugia from chronic and acute disturbance, mechanisms of resistance and recovery of coral reef ecosystems to natural and anthropogenic disturbance, coral-algal-herbivore interactions across seascapes, and biophysical processes controlling coral reef ecology. Since 2005, he has been the Coordinator for Research for the U.S. Virgin Islands Coral Reef Monitoring Program. He received his BS in marine biology from Western Washington University and his PhD in coral reef ecology from the University of Miami.

Katherine von Stackelberg is a research scientist at Harvard University and the principal scientist at NEK Associates. At Harvard, she is affiliated with the Harvard Center for Risk Analysis, the Center for Health and Global Environment, and the Department of Environmental Health. She is an expert in the development of risk-based approaches to support environmental decision-making, with an emphasis on consideration of uncertainties and ecosystem services. She has served as chair of the U.S. Environmental Protection Agency Board of Scientific Counselors, and was a member of the Scientific Advisors on Risk Assessment for the European Commission in Brussels. After receiving her bachelor's degree from Harvard University, she went on to receive a master's degree in environmental health and health policy and management, as well as a doctoral degree in environmental science and risk management from the Harvard School of Public Health.

STAFF

Emily Twigg joined the Ocean Studies Board in October 2016. Prior to her time at the National Academies of Sciences, Engineering, and Medicine, she held positions at the National Science Foundation and at the Environmental Protection Agency. She has a master's degree in environmental science and management from the Bren School at the University of California, Santa Barbara, and a Bachelor's degree in biology from the University of California, Berkeley. She has additional experience working in resource management at a national park, and in outdoor environmental education.

Andrea Hodgson is a Program Officer with the Board on Life Sciences of the U.S. National Academies of Sciences, Engineering, and Medicine. During her tenure at the Academies she has worked on a range of topics at the intersection of environmental health, risk assessment, biotechnology, biosecurity, and microbiology. Andrea's work includes convening and organizing workshops, meetings of experts, and consensus studies. She has organized workshops for and assisted in the coordination of the Standing Committee for the Use of Emerging Science for Environmental Health Decisions. Additionally, she organized the workshop *Safeguarding the Bioeconomy III: Securing Life Sciences Data* and has been involved in the following consensus studies, *Preparing for Future Products of Biotechnology* and *Environmental Chemicals, the Human Microbiome, and Health Risk: A Research Strategy*. She received her PhD in molecular microbiology and immunology from Johns Hopkins Bloomberg School of Public Health.

Trent Cummings graduated in August 2015 from The George Washington University in Washington, D.C., where he received a BA in environmental studies, sustainability. Prior to working at the National Academies of Sciences, Engineering, and Medicine, he interned with the Business Network for Offshore Wind covering the completion of the Block Island Wind Farm. He joined the Ocean Studies Board as a program assistant in December 2017.

Appendix B
Bayesian Network File Creation

In order to analyze the outputs of the biophysical model in a Bayesian network, numerical outputs of coral cover are translated to likelihood data in three steps:

First, in the MATLAB program, decadal time-slices of the output data are taken. In other words, projected coral cover (replicates of ten data points per line in the intervention table) are captured at years 2020, 2030, 2040, 2050 and 2060. Outputs are then organized according to the design table and exported to an MS Excel table. Here, output years are stored in column 1; scenarios, conditions and interventions then become grouping variables in column 2 to 8 (Figure B.1). Coral cover (the output variable) becomes the last column. Levels within each grouping variable (e.g. RCP 2.6 vs. RCP 8.5) are stacked vertically, with the number of replicate model runs (10) for each line in the intervention table (192) and numbers of time slices (5) amounting determining the number of rows in the output table (9,600).

	A	B	C	D	E	F	G	H	I
1	Years	Scenario	DeployYear	StartState	AlgGrowth	Grazing	AGF	Shading	CoralCover
2	Y2020	RCP26	Y2025	Low	Low	Low	Nil	Nil	0.131062
3	Y2020	RCP26	Y2025	Low	Low	Low	Nil	Nil	0.045066
4	Y2020	RCP26	Y2025	Low	Low	Low	Nil	Nil	0.161949
5	Y2020	RCP26	Y2025	Low	Low	Low	Nil	Nil	0.012025
6	Y2020	RCP26	Y2025	Low	Low	Low	Nil	Nil	0.247451
7	Y2020	RCP26	Y2025	Low	Low	Low	Nil	Nil	0.056783
8	Y2020	RCP26	Y2025	Low	Low	Low	Nil	Nil	0.120637
9	Y2020	RCP26	Y2025	Low	Low	Low	Nil	Nil	0.268907
10	Y2020	RCP26	Y2025	Low	Low	Low	Nil	Nil	0.222819
11	Y2020	RCP26	Y2025	Low	Low	Low	Nil	Nil	0.000002
12	Y2030	RCP26	Y2025	Low	Low	Low	Nil	Nil	0.008243
13	Y2030	RCP26	Y2025	Low	Low	Low	Nil	Nil	0.020728
14	Y2030	RCP26	Y2025	Low	Low	Low	Nil	Nil	0.049895
15	Y2030	RCP26	Y2025	Low	Low	Low	Nil	Nil	0.008082
16	Y2030	RCP26	Y2025	Low	Low	Low	Nil	Nil	0.180011
17	Y2030	RCP26	Y2025	Low	Low	Low	Nil	Nil	0.0028

NAS_BBN_v23

READY COUNT: 10 100%

Figure B.1 Screen capture of MS Excel database of coral cover output data produced by the MATLAB model. The database is subsequently imported into the software Netica for the analysis of conditional likelihoods.

Second, the database is then converted to a tab-delimited text file and imported into the software Netica (www.norsys.com) using the method described by Ni et al. (2011), but see also Nicol and Chades (2017). Briefly, in preparation for data import into Netica, an empty Bayesian network must be constructed with all independent (parent) nodes completed with titles and level descriptions identical to column headers and row information in the MS Excel file. All parent nodes should be set to discrete, i.e. using distinct levels, whereas coral cover is a continuous variable (Figure B.2).

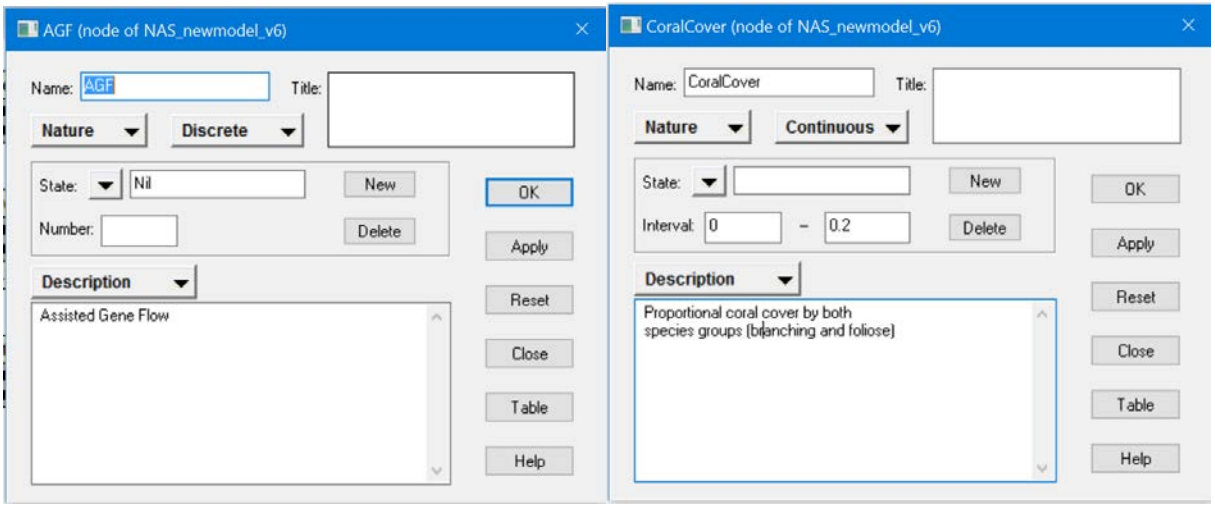

Figure B.2 Screen captures of the properties of an independent (here using AGF as an example) and the dependent node (coral cover) used in Netica. Independent nodes are set to discrete and dependent nodes to continuous.

Thirdly, the data file is imported into Netica via a learning algorithm. This process is built into Netica and can be run by importing the data file via the *Cases* tab in the menu line, then *Learn*, then *Incorporate Case File* (Figure B.3). In the subsequent menu, the user is asked to browse for the data file. Upon import, Netica converts the distributions of coral cover within and among years, scenarios and interventions to distributions of conditional likelihoods liked in the network. The Bayesian network is then ready to query.

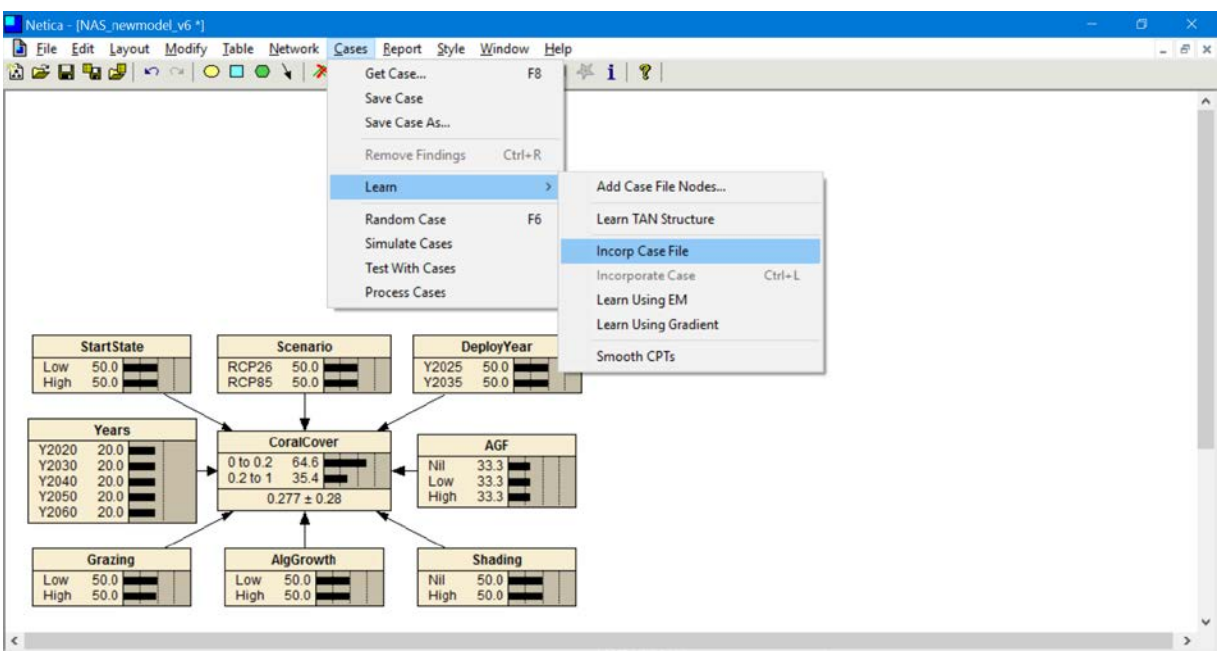

Figure B.3 Screen capture showing the route for importing the MATLAB-generated model output file into the Netica software.