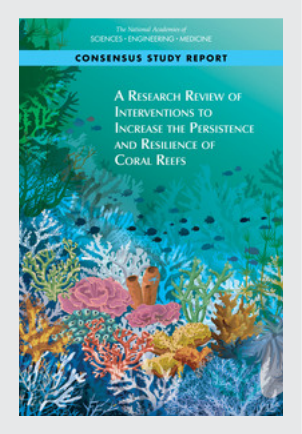

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Committee on Interventions to Increase the Resilience of Coral Reefs

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.

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Mark Baird, Commonwealth Scientific and Industrial Research Organisation
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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.

Contents

Summary

Coral reef declines have been recorded for all major tropical ocean basins since the 1980s, averaging approximately 30-50% reductions in reef cover globally. These losses are a result of numerous problems, including habitat destruction, pollution, overfishing, disease, and climate change. Greenhouse gas emissions and the associated increases in ocean temperature and carbon dioxide (CO_2) concentrations have been implicated in increased reports of coral bleaching, disease outbreaks, and ocean acidification (OA). Back-to-back mass coral bleaching events in 2015-2016 and 2017 have resulted in dramatic coral die-offs. For the hundreds of millions of people who depend on reefs for food or livelihoods, the thousands of communities that depend on reefs for wave protection, the people whose cultural practices are tied to reef resources, and the many economies that depend on reefs for fisheries or tourism, the health and maintenance of this major global ecosystem is crucial.

While abatement of local and regional stressors will continue to be critical to coral reef persistence, these efforts on their own will not be sufficient to address the impacts of climate change. The recent pan-tropical bleaching events showed that remote coral reefs under minimal influence from human activities bleached as severely as reefs exposed to multiple stressors such as pollution and overfishing. Reduction and mitigation of carbon emissions will be required for successful global management of marine ecosystems. But even with such reductions, committed warming from the current accumulation of greenhouse gases is expected to expose the majority of the world’s reefs to bleaching conditions annually by 2050. In the face of these predictions, a growing body of research on coral physiology, ecology, molecular biology, and responses to stress has revealed potential tools to increase coral resilience. Some of this knowledge is poised to provide practical interventions in the short-term, whereas other discoveries are poised to facilitate research that may later open the doors to additional interventions.

This committee has been tasked with reviewing the state of science on genetic, ecological, and environmental interventions meant to enhance the persistence and resilience of coral reefs. The complex nature of corals and their associated microbiome (the holobiont; including symbiotic algal, prokaryotic, fungal, and viral components) lends itself to a wide range of possible approaches. In this first report, the committee provides a summary of currently available information on the range of interventions present in the scientific literature. This report provides a basis for the remainder of the committee’s task to be covered in the final report. Specifically, the task in this report is to (the full task can be found in Box 1.2):

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.

Resilience refers to the overall ability of individuals, populations, or communities to respond positively after disturbance, restoring some part of their original state. As a concept, resilience can be applied to different levels of ecosystems. For example, individual organisms can show physiological resilience via survival, sustained growth, and/or reproduction (fitness). Populations can show resilience through the ability to recruit new individuals after a disturbance. Communities can show resilience in ecosystem traits such as productivity, diversity, trophic linkages, or sustained biomass through shifts in species composition. This report is structured to address the interventions that have the potential to increase resilience at each of these scales. The report also includes consideration of interventions that could promote persistence of coral reefs although they may not improve resilience, particularly those that reduce exposure to environmental stress, as an important part of the toolkit of responses to deteriorating environmental conditions. For each intervention, its attributes, current feasibility, potential scale, limitations, and risks are reviewed. Strong attention has been paid to similar efforts under way in other countries that are home to extensive reefs and strong research capacity, particularly in Australia.

Attitudes about the need for novel interventions are coalescing among managers and scientists, and the core technologies needed to enact such interventions are quickly advancing. As such, this report is a benchmark that reflects current research, identifying efforts that range from those potentially feasible now to those that offer promise on a decadal time scale. Even with these interventions, reefs at the end of this century will not look like the reefs at the beginning. The goal has been to lay out the toolbox that might allow coral reefs to persist, stabilizing the value of these ecosystems to human well-being, national economies, and future wonder.

SUMMARY OF INTERVENTIONS TO INCREASE PERSISTENCE AND RESILIENCE

Genetic and Reproductive Interventions

Managed selection is the detection of corals with above average stress tolerance, and their use in subsequent interventions. The intervention builds on the fact that coral reefs exist along a range of environmental gradients, including temperature and other stressors, reflecting the ability of individuals to acclimate, of populations and communities to adapt via selection of resilient phenotypes, and of species to adapt to one or multiple environmental pressures. These corals can be identified experimentally, by their presence in chronic extreme conditions, or by their survival after acute stresses such as mass bleaching events. Differential tolerance of corals to environmental stressors often has both a genetic component and an acclimation component. Multiple “omics” approaches (genomics, transcriptomics, proteomics, and metabolomics) help identify if phenotypic differences in corals collected from different reefs are due to fixed features.

Managed breeding is the maintenance and restoration of diverse coral reef populations through artificial propagation to achieve increased population sizes and fitness. It may take the form of *supportive breeding within populations*, *outcrossing between populations*, and *hybridization between species*. Supportive breeding within a population seeks to maintain or rebuild population diversity by augmenting local genotypes and increasing population size. The intent of performing crosses within or between species is to introduce additional genetic diversity, resulting in individuals that would have higher fitness than the parental populations or species. Managed breeding relies on the sexual propagation of corals under controlled laboratory conditions, via gamete and larval collection from the field, or through a combination of both. Success relies on high survivorship after reintroduction, and depending on management goals, demonstration of recruitment following outplanting.

Gamete and larval capture and seeding seeks to enhance the natural processes of sexual reproduction in corals by using natural spawning events to supply gametes for future use or larvae for settlement and population re-establishment or replenishment. These tools augment the reproductive strategies of other approaches, particularly managed breeding. Gametes collected in the field can be outcrossed *in situ* or in the laboratory, providing an opportunity to enhance levels of fertilization and target desirable genotypes or crosses. Larvae can be used to create chimeric colonies or hybrids. As described in the section on algal symbiont manipulation, larvae devoid of symbionts can be infected with types that convey resilience.

Coral cryopreservation is the process by which gametes, embryos, or other living materials are frozen in such a way that they remain viable after being thawed. Much of the effort for corals has focused on gamete cryopreservation, particularly sperm. However, there have been some efforts to test methods to cryopreserve embryonic material, adult tissues, and algal symbionts. Cryopreserved material can be used to increase genetic variation in critically endangered species, and it allows for fertilization between species that in nature do not live close together or that spawn at different times. Creation of viable embryos through fertilization of eggs with cryopreserved sperm is currently feasible, but other approaches are still in the development stage.

Genetic manipulation refers to the direct alteration of the genome of an organism, which may be the coral or a symbiont. Current interest in genetic manipulation is fueled by developments in CRISPR/Cas9-based genome-editing, and transcriptome-editing, that can be applied to a wide variety of organisms to generate loss-of-function mutations or to modify existing genes. With CRISPR/Cas9 methods, it may be possible to maintain the standing genetic variation at nontarget loci while propagating desirable traits into the population. There is also interest in using gene drives, which create a biased system of inheritance by enhancing passage of a selected genotype to offspring, to spread a desired alteration rapidly through the coral population. The basic mechanism of gene manipulation with CRISPR/Cas9 has been demonstrated in corals. However, there has been no demonstration of altered phenotypes from manipulation and no demonstration of incorporation of manipulated genes into an adult coral. Feasibility for enhancing coral resilience will be dependent on the identification of clear gene targets hypothesized to be able to alter coral resilience through genetics changes. In addition, the long generation time of corals will significantly lengthen the time from research to deployment. In the near term, genetic manipulation also provides an approach to experimentally identify the genetic causes of variation in stress tolerance.

Physiological Interventions

Pre-exposure is the deliberate exposure of an organism to conditions that might confer some degree of additional tolerance to subsequent re-exposure of the organism (and, potentially, its progeny) to the same or similar conditions. Evidence that pre-exposure has a beneficial effect (whether or not the specific mechanism is known) is widespread. The response of a coral to environmental stress is inherently physiological and might involve a shift in basic metabolism, cellular function, energy balance, and relationships with internal symbionts or the microbiome. Mechanisms by which these changes occur include acclimatory and adaptive changes in gene expression, epigenetic modifications, and shifts in algal symbiont communities and/or the microbiome. These responses vary in their longevity, ranging from short term (hours to days) to longer term (months to years), with certain responses potentially lasting for the entire lifespan of the coral colony (typically decades) and even being transgenerational (i.e., passed along to offspring).

Algal symbiont manipulation refers to mechanisms by which algal symbiont communities (family Symbiodiniaceae) are changed in favor of types that enhance the stress tolerance of the coral host. Although corals can often experience changes in symbiont communities following episodes of severe bleaching in the field, directed manipulations of adult corals in favor of more thermotolerant symbionts have to date only been achieved in the laboratory by duplicating these conditions. However, because the majority of corals produce gametes that do not contain algal symbionts, there are also opportunities to introduce algal symbionts during early coral life stages. A potential tradeoff in selecting symbionts that are naturally more heat tolerant, such as some members of the symbiont genus *Durusdinium*, is that their coral hosts may grow more slowly. These approaches (both at the adult and recruit stage) may also be limited by the availability of preferred symbionts in the region of interest, the specificity of symbionts to their hosts, and the longevity of the manipulated association.

Microbiome manipulation may alter the phenotype of the coral host and subsequently its fitness in response to environmental change. The microbiome in this case refers to the fungal, prokaryotic (bacteria and archaea), and viral components of the microbiome, as opposed to the algal symbiont. The microbiome can influence host coral health through facilitation of enhanced nutrient cycling; production of antibiotics; protection against stressor agents; and supply of essential trace nutrients, metals, and vitamins. The microbiome may be manipulated by shifting abundance through inoculations, adding beneficial bacteria to the holobiont, subjecting the holobiont to stress to select for adaptive microbiome members, and genetic modification. However, because very little is known about the functional attributes of the coral microbiome, targeted actions are difficult to design without further basic research.

Antibiotics can be highly effective in the prevention and treatment of bacterial (and some protozoan) diseases. Improvement in the condition of corals might thereafter increase their resilience to environmental stress. There is experience applying antibiotics at the aquarium scale, but the risk and technical limitations of applying antibiotics on a large scale inhibits readiness for broad implementation. Specifically, there is a lack of information to guide the specificity and effective dosages that are necessary to reduce the risk of antibiotic resistance. Antibiotic treatment may also affect a range of other commensal and potentially beneficial microbes, especially since lack of specificity necessitates the use of broad-spectrum antibiotics.

Phage therapy is the isolation, identification, and application of viruses that specifically target and infect bacteria. These "bacteriophages" are highly specific to the target bacterial strains, making it unlikely that other symbiotic microbes are affected. In theory, since bacteriophages are self-generating entities, one application rather than multiple applications over time may be sufficient. However, the specific dynamics and practical requirements of temporal applications have not been assessed sufficiently for corals and reefs in general. The application of large numbers of a single bacteriophage to an open reef system presents risks of uncontrolled and unintentional gene transfer events, which may have negative effects on both microbial and macroorganism dynamics. Bacteriophages also have the potential to spread virulence traits across target and nontarget hosts.

Antioxidants may be used to deplete the reactive oxygen species that are produced as a result of exposure of corals to high incident light levels, which are linked to degradation and loss of symbionts. Antioxidants would be applied during early and peak periods of environmental stress, and potentially even following the stress events to help coral recovery. The understanding of the effectiveness of this approach, although promising in early studies, is rudimentary. The risks are currently unknown; while many of the antioxidants are naturally produced compounds, application of high concentrations may have detrimental impacts on organismal function.

Nutritional supplementation of corals with carbon and other essential nutritional elements during periodic stress events can provide increased resilience, particularly by compensating for lost energy resulting from algal symbiont dysfunction caused by bleaching events. The coral aquarium trade, research facilities, and hobby aquarists routinely supplement the coral diet with a range of commercial feeds that include phytoplankton, rotifers, krill, and even pieces of shrimp, squid, or clams. However, there is currently no dedicated or robust assessment of an optimized coral diet for supplementing nutrition and building coral resilience. The addition of excess labile carbon, nitrogen, and phosphate into the reef environment may promote growth of species that may outcompete the corals or disrupt the symbiosis between corals and their algal partners.

Coral Population and Community Interventions

Managed relocation is the movement of species, populations, genotypes, or phenotypes from a source area to locations beyond their historical distribution, sometimes with different environmental parameters. There are varying goals associated with managed relocation at different scales. *Assisted gene flow* is the movement of genotypes within a population's range to support the proliferation of selected genotypes with higher stress tolerance. *Assisted migration* is the movement of individuals beyond a species' range to support movement to more favorable conditions, particularly valuable when natural dispersal is limited. *Introduction to new areas* is the introduction of stress-tolerant individuals to an area in order to maintain a coral reef community in the area. Managed relocation results in alterations to community diversity, and the cost and risk generally increase as the scale of movement increases. A key risk for all managed relocation types is the introduction of non-native pathogens, parasites, algae, microbes, commensal invertebrates, and coral predators. There is also the possibility that corals themselves become invasive. Key knowledge gaps for managed relocation generally concern what drives species distributions, species responses to novel environmental conditions, local-scale impacts of climate change, natural scales of long-distance dispersal, and the scale of local adaptation.

Environmental Interventions

Shading of coral reefs reduces their exposure to high solar irradiance, lowering peak sea-surface temperatures during warm summer months and reducing light stress, which is a co-factor in the coral bleaching response. Shading interventions may occur in the atmosphere or in the water over a reef. Clouds and aerosols can be introduced in the atmosphere to absorb and scatter solar radiation. Techniques that have been suggested for use in the water include induced turbidity, polymer surface layers, and microbubble plumes. A risk from shading is the reductions or cessation of photosynthesis, which will depend on the duration and extent of the light reduction. Consequences of aerosol injection in the atmosphere include the impact of settling aerosol (salt) particles and changes in precipitation in terrestrial or freshwater environments. Interventions that apply shading are largely limited by uncertainty in their effectiveness, control, and technical aspects of scaling up the effects.

Cool water mixing onto coral reefs is a way to reduce thermal stress by replacing or diluting warm water. Specific methods include pumps or processes that promote artificial upwelling using pipes, air lifts, or fans to partly or fully displace warm surface water with cooler water from deeper layers. While it is technically feasible to create mechanisms for artificial upwelling, these approaches are still at their testing stage, with particular questions regarding the ability to scale up. A consequence of artificial upwelling is that nutrient- and CO_2-enriched water can be introduced, leading to enhanced algal growth and acidification effects. The efficacy of artificial water mixing to reduce coral bleaching risks depends on the reef setting, geomorphology, flow direction, prevailing winds, and the oceanography and bathymetry of surrounding waters.

Abiotic ocean acidification interventions at the local reef scale alter the carbon chemistry of the seawater flowing over reefs by shifting it toward a higher pH and higher aragonite saturation state (Ω_a). Reduction of CO_2 in seawater using bubble streams with low CO_2 partial pressure builds on the principle that CO_2 in air equilibrates with CO_2 dissolved in seawater. The addition of strong bases may increase pH directly. The addition of powdered limestone has been proposed as a mechanism to enhance CO_2 uptake by the global ocean, and further as an avenue for limiting ocean acidification. Accelerated weathering of limestone is a variant of the approach, but it involves the use of CO_2 to create a local environment of low pH around a calcium carbonate ($CaCO_3$) source. Electrochemical splitting of $CaCO_3$ may also increase alkalinity, which can help to elevate Ω_a. While bubble stripping carries little risk due to its reliance on predominantly air injection, the introduction of chemicals into the reef environment carries unknown risks. Scale, logistics, resources, and infrastructure represent major constraints.

Seagrass meadows and macroalgal beds can act as OA interventions by drawing down CO_2 concentrations and elevating Ω_a in shallow-water environments on or adjacent to coral reefs. Feasibility and efficacy are location-dependent because local processes including oceanography, geomorphology, bathymetry, and currents interacting with benthic communities collectively drive seawater biogeochemistry. Whereas CO_2 levels decline during the day due to photosynthesis, they would increase at night due to respiration. Macroalgal management is likely to be preferred in coastal, nutrient-rich coral reef waters while coastal shallow-water environments are habitat better environment for seagrasses. Use of seagrasses and macroalgae have varying benefits and risks. Seagrass meadows are vulnerable to ocean warming and cyclones whereas macroalgae are generally more resilient. Additionally, seagrass meadows have high conservation value, while macroalgae are generally an indicator of degraded reef state.

Table S.1 contains a summary of the different types of coral reef interventions included in this report. Current feasibility, potential scale, limitations, and risks are estimated on the basis of current knowledge, research, or deployment, and are interrelated. For example, in most cases there is limited capacity to scale up the feasibility of most interventions to the global level without incurring increased risk.

GUIDING THEMES

Identifying versus Creating Resilience

Some corals show broad tolerance for environmental stresses, can inhabit a strong mosaic of environments, and can be associated with a diverse array of symbionts and microbes. Such variation in tolerance across populations of a species represents capacity for adaptation via natural selection. A strong component of increasing the adaptive capacity of coral reefs is to map these adaptations, understand their function in the holobiont, and use them as potential targets for enhancing population viability or for further genetic manipulation. Finding natural adaptive capacity for heat tolerance or disease resistance, for example, and using it in programs of coral outplanting or managed breeding represents a feasible, scalable approach that can potentially be undertaken in the near term on multiple species. Interventions that focus on augmenting such natural resilience may have low barriers to implementation. While not risk free, if such tolerant variants can be found locally for multiple species, then there are fewer risks than, for example, genomic manipulation or long-distance relocation. However, it is not certain that natural levels of stress resistance will prove adequate to protect corals across the extreme conditions that might occur with future climate changes. Therefore, it may be necessary to generate unprecedented genetic changes. Genomic manipulation of corals or symbionts is just beginning and faces a number of research hurdles before it can become operational.

Novel Communities

A key feature of any intervention scheme for coral reefs is the movement of coral colonies to areas where they are needed to support reef resilience. Whether new adaptive capacity is found on native reefs or generated in the laboratory, the most tolerant corals are likely to be a subset of the population. If these corals survive, then the expectation is that their tolerance is heritable and will spread. Supporting the spread of tolerant types can take several forms. First, promoting propagation and breeding can support local stress-resistant populations so that their offspring can seed other reefs. Second, moving stress-tolerant colonies to adjacent reefs can help them pass their heat tolerance to future offspring in a wider location. Third, long-distance movement of tolerant corals from laboratories or warm water regions can potentially build thermal resistance

TABLE S.1 Overview of Interventions Examined in this Report

Intervention	What It Is	Current Feasibility	Potential Scale	Limitations	Risks
Genetic and Reproductive Interventions					
Managed Selection	Creating increased frequency of existing tolerance genes	Yes 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 lab 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 lab 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

in new or depleted areas. No known long-distance introduction of corals have been done purposefully. Movement of local stress-resistant colonies over short distances likely has relatively low risks and costs, and has the best scope for upscaling. Movement of laboratory-grown coral colonies to target sites and movement of corals across large distances carry greater risks and costs.

The Value of Diversity

Coral reef ecosystems are built on diversity at the levels of species, genotypes, phenotypes, habitat, ecosystem functions, symbioses, and interactions at both macroscopic and microbial levels. Diverse populations have greater scope for adaptation and are likely to maintain abilities to respond to other stressors besides heat. Diversity supports key coral reef ecosystem services including fisheries and recreation. Interventions that focus on single species, genotypes, or symbionts may be important milestones in developing intervention technology and rescuing corals at these scales in the short term. However, sustaining coral reef ecosystems that will be exposed to a diversity of stressors will require multispecies approaches and consideration of the broad suite of both biological and ecological processes that underpin ecosystem resilience.

Ecological Tradeoffs

Interventions that target a particular resilience trait may necessitate a tradeoff. For example, symbionts that are naturally more heat tolerant, such as those in *Durusdinium*, impart greater heat tolerance to their coral hosts but may result in slower coral growth rates, reduced reproductive output, and greater disease susceptibility. Additionally, reducing the diversity of genotypes through genetic interventions reduces the ability to adapt via natural selection to future stresses. Multiple stressors are often associated with coral declines, and the inability to respond to multiple stressors is a risk to reef persistence. Interventions that reduce the light incidence may reduce photosynthetic activity of coral and other nearby organisms such as seagrasses. Artificial upwelling of cool water may lead to both nutrient and CO_2 enrichment from deeper waters.

The Complex Holobiont

Corals and their algal and microbial symbionts are a unit that responds uniquely to stress depending on the coral and symbiont genomes and the mix of microbes that live on and within the colony. Alteration of symbiont communities is known to increase heat tolerance for some corals, but with very different levels of empirical evidence. Manipulating each of these poses very different barriers to implementation, different levels of permanence, and different needs for technology development. They also impose different risks. Parallel efforts in native gene discovery, physiological testing, genetic manipulation, and selective breeding will be important investments.

Achieving Scale

The spatial and temporal scales upon which interventions must operate depend on conservation goals, usually related to maintaining a certain level of local diversity and/or ecosystem services.

To date, most interventions have operated at experimental or local scales, impacting a limited number of individuals. Some have the potential to be produced and applied at reef scales, including atmospheric shading or application of probiotics, antibiotics, antioxidants, and nutritional supplementation. However, delivering these interventions with specificity, reduced risk, and at the required scale still has significant knowledge barriers. Others rely on large-scale efforts, at least at first, to achieve results beyond the individual. This encompasses efforts that require relocation or managed breeding in the laboratory and outplanting.

On the temporal scale, the effect of an intervention may be either permanent or self-perpetuating across generations, or it may be temporary, requiring either continuous or periodic reapplication during times of stress. Genetic interventions are intended to perpetuate themselves to future generations (unless they are limited to an epigenetic response), although it is likely that a degree of captive breeding and release could continue to be necessary. Physiological interventions affecting individual coral holobionts are generally not permanent and are unlikely to convey resilience to future generations. Managed relocation of coral individuals, if successful, has the potential to remain permanent.

Engineering the Local Environment

Although the increase in average long-term ocean temperatures chronically stresses corals, bleaching events result in acute impacts that are concentrated in the summer period of weeks or months. These acute reactions to abnormally high temperatures might be reduced by transient, local manipulation of the heat or light environment. Furthermore, ocean acidification may become a chronic and significant impact on corals in the future. Potential engineering solutions to these problems are being explored, but none are ready to be deployed on anything but an experimental scale. Additionally, the spatial scale at which they will ultimately have impact is a lingering question. Nevertheless, the ability to deploy this type of transient protection in the future may be important to protect high-value reef environments on local scales.

CONSIDERATIONS FOR IMPLEMENTATION

The interventions discussed in this report have not been implemented beyond experimental scales in the field, if at all, making their efficacy and impacts uncertain. Adaptive management can help account for and resolve key uncertainties in management practices that have uncertain results, and thus is important for assessing the readiness of interventions for implementation at meaningful scales and their ability to meet conservation goals. Careful planning and monitoring of interventions, including the development of model-based expectations, can ensure that projects maximize learning to enhance benefits and reduce risk.

These interventions have varying degrees and likelihoods of benefits and risks. They alter the environment with consequences that cannot completely be foreseen given the current state of knowledge. While adaptive management provides a structured way of improving understanding of these benefits and risks, even this cannot be implemented without the decision to deploy these interventions in the ocean at least at an experimental scale. The task for this report is to synthesize current knowledge and lay the groundwork for informed decisions about conserving coral reefs under climate change. The remainder of the committee’s task, to be documented in a subsequent report, is to provide a framework for evaluating the relative risks and benefits of implementing these interventions. Additionally, the committee will develop a decision pathway to guide progress of these interventions from the research phase to implementation, when and where appropriate. Such a framework can be used to identify intervention strategies for which the consequences and costs may be justified. While it is not the committee’s task to consider the social, policy, legal, and ethical considerations of implementing these approaches, these will be important to decision-makers as well.

1

Introduction

Coral reef declines have been recorded for all major tropical ocean basins since the 1980s, averaging approximately 30-50% reductions in reef cover globally, with spikes after the 1998 global coral bleaching event (Selig et al., 2012; Figure 1.1a). These losses derive from a host of problems experienced by coral reefs around the world, including coastal habitat loss, pollution, overfishing, and climate change. Recent losses of coral cover have increased dramatically following the double global bleaching events of 2015-2016 and 2017 (Hughes et al., 2017a, 2017b, 2018; Figure 1.1b), driven by an extensive and prolonged ocean warming event (NOAA, 2017). Because coral reefs are integrated ecosystems, declines of reef-building corals and their associated three-dimensional complexity tend to also lead to declines of other species that depend on healthy reefs (Bellwood et al., 2006), such as a large number of coral reef fish (Graham et al., 2007), reducing the ecosystem services provided by coral reefs. For the hundreds of millions of people who depend on reefs for food or employment (Cinner et al., 2012; Moberg and Folke, 1999), the thousands of communities that depend on reefs for wave protection (Ferrario et al., 2014; Sheppard et al., 2005), and the many economies that depend on reefs for fisheries or tourism (Costanza et al., 2014; Hoegh-Guldberg et al., 2015), the health and maintenance of this major global ecosystem is crucial.

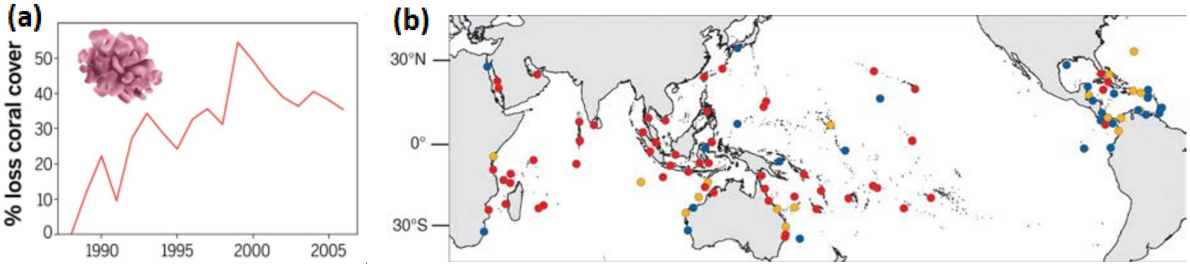

FIGURE 1.1 (a) Percent loss of global coral cover over the 20 years prior to 2007 from a variety of causes. SOURCE: McCauley et al., 2015, using data summarized in Selig et al., 2012. (b) Coral bleaching in 2015 and 2016. Red markers denote reefs where >30% of corals were bleached. Orange markers denote areas where bleaching affected <30% of corals. Areas with blue markers showed no recorded bleaching in 2015 and 2016. SOURCE: Hughes et al., 2018.

Anthony et al. (2015) divided the discussion of the ways coral reefs are impacted by humans into press and pulse stressors. Press stressors include pollution, sedimentation, overfishing, ocean warming, and acidification, because these factors exert long-term steady pressure on coral growth, survival, and reproduction. Pulse stressors include storms, bleaching events, or disease outbreaks that are more acute, periodic, and destructive over short time periods. Some press stressors are local (e.g., pollution), and some affect large regions, driven by global climate change (chronic warming and acidification). An effort to sustain coral reefs in the future calls for conservation and management strategies that can underpin the biological and ecological processes that build tolerance and resilience to multiple stressors (Anthony et al., 2017).

GLOBAL CLIMATE STRESSORS

Increasing changes in the global climate and ocean chemistry threaten the persistence of coral reefs. An understanding of these impacts is important for identifying the processes that interventions may target. Additionally, variable responses of coral to stressors provide insight into potential natural resilience to these stressors. It should be noted that mitigation of global stressors is important for preserving coral reefs, and, compared to novel interventions that target the resilience of coral reefs, has high certainty in effectiveness. Mitigation of global stressors will also inevitably increase the likelihood of any local intervention succeeding.

Temperature Stress

By far the most attention has been paid to the global effects of ocean warming on coral health. The link between temperature and corals derives largely from the bleaching response of coral cells to higher than normal temperatures (Box 1.1). Recent increases in ocean temperature have led to a significant increase in exposure of corals to high-temperature events (Figure 1.2) and have caused severe coral loss globally (reviewed in Hughes et al., 2018). Comparative analysis of bleaching patterns and temperatures shows that some corals are more resistant to bleaching than others (especially species in the genus *Porites*, see Carpenter et al., 2008; Marshall and Baird, 2000). Comparisons also show that the temperature at which bleaching occurs is relative to the temperature regime at a specific location, even for the same species (Glynn, 1996). These observations have led to a widespread rule of thumb that bleaching starts after temperatures exceed the maximum average summer temperature for a region. The longer these high temperatures persist, the more likely bleaching becomes. Thus, bleaching susceptibility typically is be linked to the sum of excess degrees of heat over weeks of exposure (measured by the National Oceanic and Atmospheric Administration's [NOAA] Coral Reef Watch program as Degree Heating Weeks). Bleaching events can be driven or amplified locally or regionally by ephemeral atmospheric systems that promote calm and clear conditions (e.g., doldrums conditions) that favor ponding of warm water masses and deep light penetration (which aggravates the effects of high temperature).

Recovery from bleaching depends on the severity of the heating event (duration and degree of temperature increase) and the condition of the corals. During strong temperature pulses, or when colonies are less able to capture food, coral death is common (Grottoli et al., 2006). In milder bleaching events, or when corals have abundant energy reserves (Connolly et al., 2012), recovery can be widespread. Even in these cases, full recovery of physiological homeostasis, growth, and reproduction lags behind recovery of symbiont density for months (Grotolli et al., 2006; Thomas et al., 2018). Following long recovery periods, the ability of colonies to survive another bleaching event is curtailed and may also result in subsequent increased disease within the population. Back-to-back El Niño events in 2015 and 2017 led to widespread coral loss, especially among colonies impacted by the second event but not yet recovered from the first (Thomas et al., 2018).

Cellular mechanisms of coral bleaching are much less understood than ecological patterns of bleaching. Bleaching induced by temperature appears to largely involve active ejection of

BOX 1.1
Coral Bleaching

The phenomenon of coral bleaching is visible when colonies turn from their normal tan, gray, or green color to a stark white. These corals are not dead. Instead, individual polyps that make up the coral colony have ejected their internal single-celled algal symbionts, also known as zooxanthellae (from the dinoflagellate family Symbiodiniaceae; see LaJeunesse et al., 2018) as a response to environmental stress, leaving largely transparent tissues covering their white skeletons. Bleaching reactions are most commonly driven by temperature extremes, tending to occur at temperatures 1-2°C above the normal maximum summer temperatures, increasing in likelihood the longer the temperature extremes last. While high-temperature extremes are a more common and growing occurrence, bleaching is also known to occur when temperatures fall below a coral's minimum thermal threshold (Hoegh-Guldberg and Fine, 2004; Roth et al., 2012). Because corals depend on photosynthesis taking place in the symbiont for much or most of their food, bleached corals are deprived of the energy they need for normal growth or reproduction (Glynn, 1996). Colonies without abundant external food supplies or energy reserves typically die after bleaching, but others can recover and repopulate with symbionts (Grotolli et al., 2006). Full physiological recovery as evidenced by transcriptome patterns can take months after recovery of symbiont densities; recovery of growth rates and reproduction can require more time (Thomas et al., 2018).

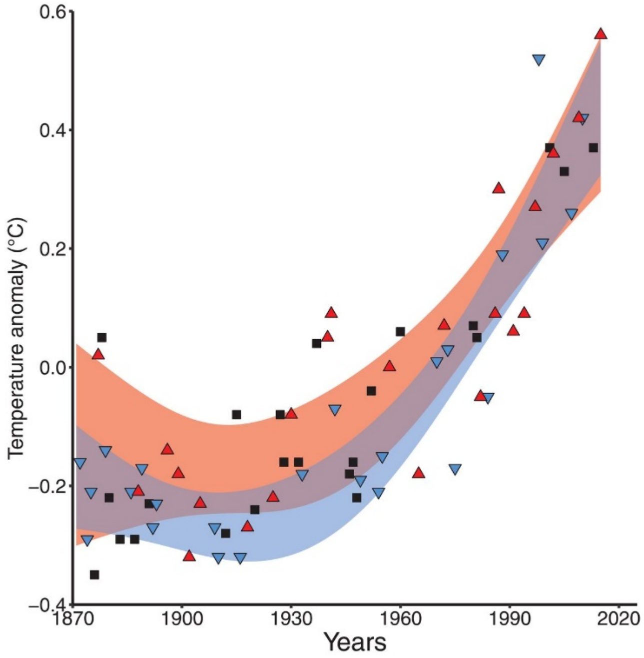

FIGURE 1.2 Ocean temperatures have increased dramatically since 1930. Sea surface temperature anomalies within 100 coral habitats are compared to the 1961-1990 average. Red triangles denote El Niño years whereas La Niña and non-ENSO (El Niño-Southern Oscillation) years are blue triangles and black squares, respectively. 95% confidence intervals are shown for El Niño and La Niña conditions (red and blue shading, respectively). SOURCE: Hughes et al., 2018.

symbionts from coral cells, rather than strict loss of symbiont-containing coral cells or death of coral cells (Weis, 2008). Bleaching is widely associated with impairment of symbiont photosynthesis, especially disruption of the electron transport chain delivering the energy of captured photons to carbon-fixing centers in the chloroplast. This breakdown occurs at about the same time as reactive oxygen species (ROS) are released in the cells, either through production by malfunctioning chloroplasts or in mitochondria (Downs et al., 2002; Baird et al., 2009b). Thus, high temperature promotes the dysfunction of cellular proteins involved in photosynthesis. Additionally, light (specifically, photosynthetically active radiation at wavelengths that promote photosynthesis) induces electron flow in symbiont chloroplasts that causes a buildup of ROS that can impair cell function (photo-oxidation; Lesser, 2011). In addition, components of solar radiation that do not contribute to photosynthesis, such as ultraviolet light, have also been implicated in bleaching (Gleason and Wellington, 1993; Lesser, 1997). Light is therefore a co-factor in initiating the coral bleaching response (Baker et al., 2008). Coral cells undergo a range of responses, including production of heat shock and chaperone proteins that refold proteins damaged by heat (Barshis et al., 2013; DeSalvo et al., 2008, 2010; Meyer et al., 2011), proteins that remove reactive oxygen (Lesser, 1997; Weis, 2008), as well as a large number of transcription factors that serve in cellular signaling (Traylor-Knowles et al., 2017).

Despite these detailed studies, the stress trigger that induces coral cells to initiate ejection of the symbiont remains unknown. Some indications are that the cellular mechanism controlling programmed cell death (apoptosis) may be involved because of the changes in apoptosis-related genes during bleaching (Weis, 2008). Alternatively, other mechanisms including cell detachment (Gates et al., 1992) might be at the heart of this phenomenon. The unfolded protein response is a basic eukaryotic cellular mechanism to increase protein folding in times of stress (see Oakley et al., 2017), but it may induce cell death after severe heat stress and bleaching (Ruiz-Jones and Palumbi, 2017). Such fundamental cellular stress responses could underlie coral bleaching if the switching mechanism used for the unfolded protein response was linked to the bleaching threshold (Ruiz-Jones and Palumbi, 2017).

The cellular mechanism that causes bleaching appears to have different environmental thresholds for corals of different species, and for corals housing different species of internal symbiotic algae. Within species, even those with the same symbionts, different coral colonies can have different bleaching tolerances. Field observations, transplants, and laboratory studies have shown that some of the variation among colonies is due to the widespread ability of corals to acclimate to local or seasonal heat conditions (Palumbi et al., 2014; Ainsworth et al., 2016). Other shifts in susceptibility to bleaching are associated with changes in the symbiont after bleaching events (reviewed by Baker et al., 2004; Silverstein et al., 2015). A strong source of variation among colonies also resides in the genetic or epigenetic differences between populations selected for living in different microhabitats. The genetic underpinnings of these differences are not well known, but appear to include many genes. Dixon et al. (2015) showed that hybrids of warm- and cool-water-adapted corals from the Great Barrier Reef exhibited intermediate heat tolerance. Bay and Palumbi (2015) used transcriptome scans to uncover more than 100 genes associated with populations living in a warm water, back reef pool in Samoa. By contrast, Jin et al. (2016) showed strong effects at a single genetic locus for antioxidant capacity. Although detailed study of the genetic mechanisms of coral bleaching or heat tolerance is still in progress, little evidence currently exists to suggest that there are a few master genes of large effect controlling heat tolerance in many species.

Ocean Acidification

A second global stressor related to climate change is the gradual acidification of the oceans because of increasing carbon dioxide (CO_2) levels in the atmosphere (e.g., Doney et al., 2009). CO_2 emitted into the atmosphere from fossil fuel combustion forms carbonic acid when it dissolves in the ocean. This causes a decrease in pH and decline in carbonate saturation (Caldeira and Wickett, 2003), resulting in a lower aragonite saturation state (Ω_a) (Kleypas et al., 1999, 2006; Raven et al., 2005). Lower pH, increasing CO_2, and decline in Ω_a have complex effects on reef-building corals. Long-term exposure to low pH reduces calcification and growth rates (Albright et al., 2018; Chan and Connolly, 2013; Kleypas and Yates, 2009; Langdon et al., 2000; Pandolfi et al., 2011), with a reduction in calcification of 15-22% per unit decrease in the Ω_a of seawater.

The projected fall in pH and Ω_a as CO_2 levels increase (e.g., Figure 1.3) suggests long-term declines of coral reefs (Chan and Connolly, 2013; Hoegh-Guldberg et al., 2007) as CO_2 emissions build up in ocean waters. However, unlike thermal anomalies, ocean acidification (OA) is a gradual buildup of a chronic stress that does not manifest as acute events. Also, coral reefs modify their seawater carbon chemistry through calcification (Kleypas et al., 2011), complicating the attribution of local impacts to ocean acidification. During the Anthropocene, the mean pH of the global ocean has dropped by about 0.1 units, lowering the mean Ω_a in coral reef waters by more than half a unit (Cao and Caldeira, 2008). If atmospheric CO_2 were allowed to double relative to pre-industrial levels (560 ppm), mean Ω_a in coral reef waters would drop another full unit. Recent work on the southern Great Barrier Reef demonstrates that OA has already caused an approximately 6% drop in reef calcification (Albright et al., 2016). Other consequences of OA for reef corals include reduced coral fertilization and recruitment (Albright and Langdon, 2011), increased fragility of coral skeletons (Tambutté et al., 2015), and increased risk of reef wave damage by storms (Madin et al., 2008), the latter in part caused by accelerated bioerosion of the reef substrate (DeCarlo et al., 2015; Wisshak et al., 2012). As OA directly impacts two key fitness components of corals—growth and reproduction (Anthony, 2016) —any interventions that can counteract OA will directly support reef resilience.

The reactions of corals to increased CO_2 levels and decreased pH varies among species. A study of coral reefs near natural CO_2 vents in Papua New Guinea and Mexico shows that species of *Porites* tend to be dominant nearest the vent locations (Fabricius et al., 2011), with colonies exhibiting reduced calcification rates (Crook et al., 2013). At other sites such as Nikko Bay in Palau, high concentrations of CO_2 combined with high temperatures result in reef areas dominated by *Porites* and a few other genera that maintain high growth rates. Laboratory studies also show increased ability of these corals to calcify under high CO_2 levels (Shamberger et al., 2014). The ability of some corals to calcify under a variety of pH levels has been traced to their ability to maintain high pH at the site of calcification. For example, as external seawater pH dropped from 8.1 to 7.2, the pH of fluids at the local sites of calcification in *Porites* corals dropped only from 8.5 to 8.2 (McCulloch et al., 2012). Other studies suggest that ample external food supply allows coral calcification to be maintained despite higher metabolic costs of calcification under low pH conditions (Drenkard et al., 2013).

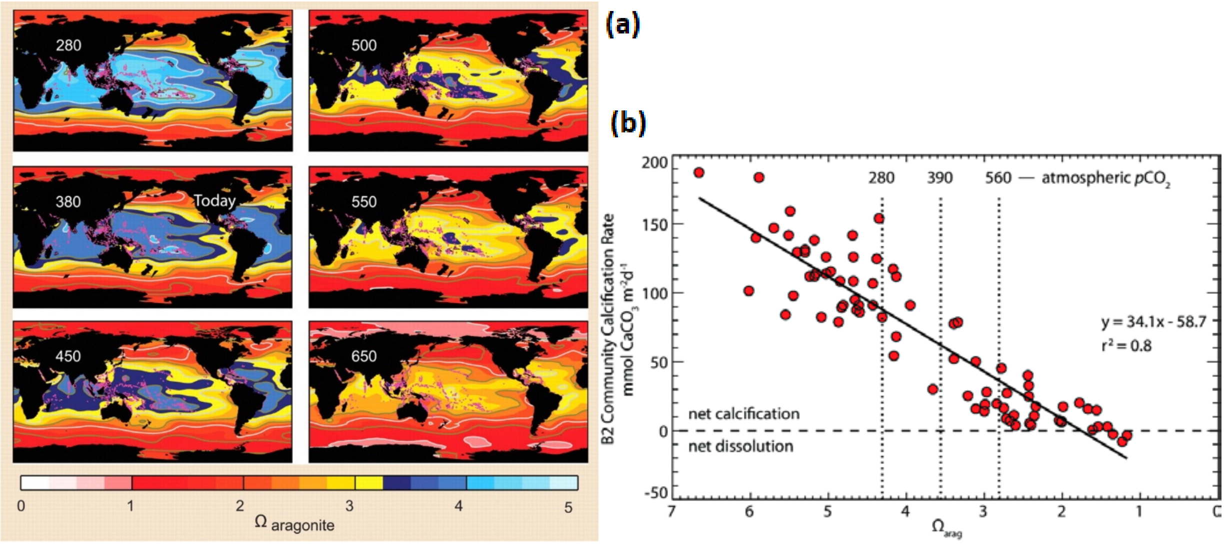

FIGURE 1.3 (a) Predicted aragonite saturation states (Ω_a) for global surface waters as CO_2 levels increase. Numbers in white text in the upper left of each panel show various CO_2 levels in ppm. SOURCE: Hoegh-Guldberg et al., 2007 (b) Community calcification rates in the Biosphere 2 coral reef mesocosm as aragonite saturation changes. SOURCE: Kleypas and Yates, 2009; data by Chris Langdon

DISEASE

Increased reports of coral disease outbreaks have been associated with warming events as well as local stressors (Carpenter et al., 2008; Harvell et al., 2007). In the Caribbean specifically, disease outbreaks affecting both corals (often white-band disease initially) and a key reef herbivore, the urchin *Diadema antillarum* were instrumental in driving declines in coral cover (Aronson and Precht, 2001a, 2001b; Lessios, 2016). The rapid loss of corals in the Caribbean from disease outbreaks is unprecedented in the geological records (Aronson and Precht, 2001a; Gardner et al., 2003), altering both the total abundance and diversity of coral species (Weil, 2004). Because diseases agents often infect the frame-building corals, the destruction of the reef habitat due to disease also affects other members of the coral reef ecosystem (Nugues, 2002).

Disease outbreaks within ecosystems often occur when thermal thresholds are surpassed, making corals among the most susceptible due to a very narrow thermal threshold for optimal coral health (Harvell et al., 2002). Randall and van Woesik (2015) linked increase of sea surface temperatures (SSTs; both thermal minima and maxima) with the spread of white-band disease, which contributed to the region-wide declines of the dominant Caribbean reef-building coral, *Acropora palmata* and *A. cervicornis*. Bleaching extent has been found to correlate with disease incidence (Brandt and McManus, 2009). In other regions, similar links between thermal stress and coral disease outbreaks have been reported (Bruno et al., 2007). Importantly, future climate scenarios have been projected to result in increased disease outbreaks, impacting coral populations globally (Fabricius, 2005; Harvell et al., 1999, 2002; Maynard et al., 2015). Factors such as nutrient enrichment and increased sedimentation linked with rapid urbanization and coastal development can also exacerbate disease impacts on reefs (Bruno et al., 2003; Pollock et al., 2014; Vega Thurber et al., 2014). For example, field and laboratory experiments have demonstrated that moderate increases in nutrient concentrations (phosphorus, nitrate, and ammonium) can substantially increase the severity of some diseases, through both higher prevalence and increased lesion progression rates (Bruno et al., 2003; Vega Thurber et al., 2014; Voss and Richardson, 2006; Wang et al., 2018). Similarly, by stressing corals, sediments may make the corals more susceptible to infections by microbial pathogens and may also act as disease reservoirs (Voss and Richardson, 2006). Coinciding with the emergence of coral diseases, many coral reefs have experienced dramatic increases in benthic macroalgae (Ceccarelli et al., 2018; Edmunds, 2002; Hughes, 1994; McCook, 1999). Elevated dissolved inorganic carbon levels derived from algal exudates can accelerate the growth rate of microbes in the coral's surface mucopolysaccharide layer by an order of magnitude, which impacts coral health through disruption in the balance (dysbiosis) between the coral and its associated microbiota (Kline et al., 2006). Macroalgae may also act as disease reservoirs as was found in the Caribbean, where corals that were in contact with the algae *Halimeda opuntia* developed disease symptoms (Nugues et al., 2004).

Disease is a natural part of any ecosystem; interactions between the host and the disease agent are a constant arms race that help shape patterns of species evolution (Rosenberg et al., 2007). The surrounding environment has a strong influence on disease dynamics within animal populations, either through reducing the resilience of the host or promoting the pathogenicity/virulence of a causative agent (Plowright et al., 2008). An increase in disease prevalence within coral populations is therefore an indicator of stress on the reef ecosystem. Ocean warming or human-driven environmental perturbation affect basic biological and physiological properties of coral, thus influencing the balance between opportunistic pathogens and the coral's ability to prevent pathogen infection or overcome abiotic challenges (Ben-Haim et al., 2003; Harvell et al., 2002; Rosenberg and Ben-Haim, 2002). Currently, understanding of the interactions at the cellular level between the disease agents, the coral immune system, and environmental factors is poor and inhibits attribution of disease causation (Mera and Bourne, 2017). For successful management of disease outbreaks and therefore ensuring the long-term resilience of coral populations in both natural ecosystems and artificially reared coral systems, a more thorough understanding of the underlying biotic, abiotic, host, and environmental factors leading to disease onset is still required. Nevertheless, the clear links between anthropogenic stresses on reefs and higher disease prevalence highlights that as we move to climate regimes outside previously experienced thresholds, the potential for diseases to impact coral populations at broad ecosystem scales increases as well.

LOCAL STRESSORS AND STRESS PREVENTION

Because of the high severity and widespread occurrence of local human pressures on coral reefs, there have been many studies, and decades of effort, to measure the impact and mitigate the effect of human activities on reef ecosystems. Despite the impact of bleaching on coral cover (Hughes et al., 2017b), historically the majority of coral losses have been ascribed to non-climate-related coral reef changes, such as local habitat destruction, overgrowth by algae after overfishing, pollution, and sedimentation (Bellwood et al., 2004; Pandolfi et al., 2003). It is not the purpose of this report to summarize these many papers and decades of work. However, the role of local stressors on reefs interacts with the role of climate (e.g., Carilli et al., 2009; Hughes et al., 2017a), and so local efforts to support reef ecosystems will always be a substantial part of any global reef protection strategy.

A recent summary for the Great Barrier Reef, for example, shows that local effects of human activity on reefs include strong impacts by overfishing, habitat destruction, pollution from land, and sedimentation, which may result from coastal development, transportation, aquaculture, and other activities (Table 1.1; Uthicke et al., 2016). Similar conclusions have been made for the Caribbean (Jackson et al., 2014). Because of the importance of local stressors on corals, and the links between local impacts and global climate change, some key findings about local impacts are briefly summarized here. In each case, interventions that address the source of local stressors have been identified, and in some cases, stressors have been mitigated. Despite decades of understanding the nature and extent of these local stressors in causing coral reef health declines (e.g., Russ et al., 2015), it remains challenging for local jurisdictions to solve these problems (Aswani et al., 2015). Also, the recent pan-tropical bleaching events of 2015 and 2017 showed that remote coral reefs under minimal influence from pollution and overfishing bleached as severely as reefs exposed to multiple pressures (Hughes et al., 2017b). Therefore, while local- and regional-scale management of local stressors will continue to be critical under climate change because it reduces chronic mortality and facilitates recovery from pulse stressors, these efforts on their own are inadequate in the face of ongoing climate change (Anthony, 2016).

Overfishing: Fish impact coral health through many mechanisms (Hixon, 2015; Mora et al., 2011; Mumby et al., 2007). A primary role is that of herbivorous fish in preventing fast-growing algae from over-growing corals (Hughes, 1994; Hughes et al., 2010; Jackson, 1997). When herbivory declines, macroalgae quickly grow, overwhelming corals (e.g., McCook, 1999) and potentially preventing settlement of coral larvae (Davies et al., 2013). As a result, loss of herbivores through local fishing pressure can result in a phase shift from coral-dominated to algal-dominated reefs (Hughes, 1994). The role of some herbivorous species such as parrotfish has been so great that their abundance has been suggested as a major indicator of reef health (Jackson et al., 2014; Mumby et al., 2007). However, a series of studies suggests that the relationship between herbivory and coral health is contingent on other environmental factors, such as the species involved, the location (Adam et al., 2015; Russ et al., 2015), and nutrient load (e.g., Burkepile et al., 2013).

Beyond traditional fisheries management strategies of effort and size limit controls, two broad categories of management approaches can reduce the likelihood of overfishing: marine protected areas (MPAs) and rights-based fisheries. MPAs address the ecosystem impacts of fishing by restricting or eliminating fishing in designated areas (McClanahan et al., 2006; Pikitch et al., 2004; Soler et al., 2015). On average, MPAs lead to increases in density, biomass, body size, and diversity compared to before MPA establishment or outside MPAs (Lester et al., 2009), and MPA networks on the Great Barrier Reef support coral resilience through a suite of processes (Mellin et al., 2016). Meta-analyses have suggested key features of MPA management that increase their effectiveness in nearshore fisheries recovery including implementation of no-take areas, effective enforcement, and engagement of local fishers in planning and implementation (Di Franco et al., 2016; Edgar et al., 2014). Rights-based fisheries management can incentivize sustainable resource use and environmental stewardship by providing ownership over a share of the total fishery quota (catch shares or individual transferable quotas, or ITQs; Copes, 1986, Costello et al., 2008) or ownership over a region through membership in a small collective (territorial user rights for fishing, or TURFs; Gelcich et al 2010; Jentoft et al., 1998). Observed benefits of ITQs include reduced variability in fishing and less discards (Essington, 2010), and observed benefits of TURFs include greater abundance and size of harvested species as well as greater biodiversity (Gelcich et al., 2010).

TABLE 1.1 Characterization of Stressors to Coral on the Great Barrier Reef

Pressure/Threat	Local (L) vs. Global (G) Causes	Acute (A)/ Chronic (C)	Risk to Ecosystem
Ocean warming	G	C/A	Very High
Ocean acidification	G	C	Very High
Cyclones/altered weather patterns	L (G)	A/C	Very High
Illegal fishing and poaching	L	C	Very High
Incidental catch of species of conservation concern	L	A	Very High
Nutrient runoff	L	C/A	Very High
Outbreak of Crown of Thorns Seastars	L	A	Very High
Sediment runoff	L	C/A	Very High
Coastal habitat modification	L	C	Very High
Sea level rise	G	C	Very High
Pesticide pollution	L (G)	C/A	High
Barriers to flow	L	C	High
Discarded catch	L	A	High
Extraction of predators	L	A/C	High
Disposal of dredge material			
Marine debris	L (G)	A/C	High
Extraction from spawning aggregators	L	A/C	High
Outbreak of disease	L (G)	A	High

SOURCE: Recreated from Uthicke et al., 2016.

Habitat destruction: Direct impacts of fishing on coral reefs include blast fishing (McManus et al., 1997) and trawling (Hall-Spencer et al., 2002) or pull seining (McClanahan et al., 1997) that cause physical damage to the reef structure via detonation of explosives or dragging of nets through reefs. Reefs are also destroyed for facilities development (e.g., ports and airports) or to provide building materials. In addition, indirect reef destruction occurs through increases in sedimentation associated with coastal development, pollution, and other kinds of deleterious human impacts. Habitat destruction can also occur from overharvesting colonies for the aquarium trade or nursery construction, and from damage from tourism (Davenport and Davenport, 2006). Protecting local reefs from habitat destruction can be an important way to protect ecosystem diversity (White et al., 2000).

Water quality: Growth, survival, reproduction, and recruitment of corals are strongly influenced by water quality including turbidity, sediments, nutrients, and toxic pollutants. Particular attention has been paid to nutrient enrichment, sewage, petroleum products, and metals (Dubinsky and Stambler, 1996; Fabricius et al., 2005), and many other local pollutants have been shown to negatively affect corals (Duprey et al., 2016; Loya and Rinkevich, 1980; Walker and Ormond, 1982; Wenger et al., 2016; Wilkinson, 1999). Sources of pollution range from human sewage systems, farm runoff, golf courses, urban development, waste deposition, oil and gas leakage, livestock pens, and many other human activities, even use of sunscreens (Downs et al., 2016; Pandolfi et al., 2005). Effective mitigation of pollution, typically at a local level, is key to reducing or reversing these problems (e.g., Wear and Vega Thurber, 2015).

Sediments broadly affect corals through smothering, especially when sediment loads are high after storms or coastal construction (reviewed in Fabricius, 2005; Richmond et al., 2007). There is also evidence that sediments can reduce egg-sperm interactions, thereby decreasing fertilization success (Humanes et al., 2017), inhibit settlement (Babcock and Smith, 2000; Hodgson, 1990; Perez et al., 2014) and decrease the likelihood of juvenile coral survival (Babcock and Smith, 2000; Richmond et al., 2018). Sediment and turbidity may reduce light reaching symbiotic zooxanthellae and increase prevalence of coral disease and other indicators of poor coral health (Pollock et al., 2014).

Nutrients in the sediment that dissolve in seawater as well as from other effluent sources can contribute to eutrophication and algal growth, primarily when algae are otherwise nutrient-limited. However, the effect of eutrophication on coral is not strictly deleterious, and its impact will be ecosystem-dependent (D'Angelo and Wiedenmann, 2014; McCook, 1999; McCook et al., 2001). Turbidity due to sedimentation also decreases the ratio of photosynthesis to respiration (Junjie et al., 2014; Philipp and Fabricius, 2003;Telesnicki and Goldberg, 1995). However, because particulate matter is a source of both nutrients and carbon in addition to providing shade, moderate turbidity can potentially provide an energetic and light reduction benefit for corals during or after bleaching (e.g., Anthony et al., 2007, 2009). Erosion-prevention techniques to reduce turbidity include halting deforestation and planting seagrass or scrub brush on dunes. Construction, farming and coastal use practices that minimize erosion have also been successful (Gibson et al., 1998).

Storms: Tropical cyclones or hurricanes are a natural part of the disturbance regime on coral reefs (Connell, 1978; Connell et al., 1997; Rogers, 1993). Recovery from storm damage has classically been a way that coral reef communities have been thought to maintain high levels of diversity in the face of competition for space. Tropical summer storms often follow repeated storm tracks, and so certain reef areas experience more frequent and more severe storm damage (Wolff et al., 2016). In some cases, typhoons during warm water events can reduce bleaching (e.g., Bernardo et al., 2017; Manzello et al., 2007). However, storms can cause massive damage and long-term losses of coral when recovery is low (Gardner et al., 2005; Woodley et al., 1981).

Storm damage varies dramatically on a local scale but is not due to local stressors. The number and severity of strong storms is thought to be increasing with climate change, but such links are difficult to apply to any given storm (NASEM, 2016b). While infrastructure has been developed to protect human communities from storms, few interventions have been documented for protecting coral reefs. It is worth noting here that healthy coral reefs provide natural coastal protection against storm waves (Ferrario et al., 2014), an ecosystem service worth trillions of dollars on a global scale (Beck et al., 2018; Costanza et al., 2014).

Invasive species: Traditionally, marine invasive species have been considered to be more of a problem in low-diversity environments such as estuaries, rather than on coral reefs. Nevertheless, some high-profile cases of invasive species on coral reefs have raised awareness of this threat. When invasive species cause major physical, chemical, or biological changes, they set in motion the establishment of fundamentally novel communities. Most notorious is the lionfish (*Pterois* spp.) invasion of the tropical Atlantic; what started with a few observations in Florida has in less than two decades resulted in the establishment of populations ranging from the northwest Atlantic, the Gulf of Mexico, and the Caribbean to Brazil and from shallow waters to mesophotic reefs. They are considered a major problem because they are voracious predators of juvenile reef fish (Hixon et al., 2016), which is of particular concern because of the widespread prevalence of overfishing in these regions.

However, lionfish are not the only invasive species on reefs. It has been estimated that 23% of the species reported for Pearl Harbor in Hawaii are potentially non-native (Coles et al., 1999). Invasive seaweed species have become established in a variety of locations including Florida (LaPointe and Bedford, 2010) and Hawaii (Martinez et al., 2012), and the eastern Caribbean has been invaded by a non-native seagrass (Scheibling et al., 2018). There are several species of invasive *Tubastrea* corals in the Atlantic (e.g., Luz and Kitahara, 2017), and the now globally distributed, temperature-hardy symbiont *Durusdinium trenchii* (formerly *Symbiodinium* clade D) is thought to be an invader in the Caribbean (Pettay et al., 2015). Recently, even terrestrial invaders have been shown to harm coral reefs; rat-plagued islands in the Indian Ocean have fewer seabirds, which in turn results in a variety of impacts on the surrounding reefs, including fewer nutrients and fewer algae-eating fish (Graham et al., 2018).

In the context of restoration, invasive species, once established, are essentially impossible to eradicate. Efforts to mitigate the effects of invasive species often rely on volunteer efforts, are labor intensive, are expensive (e.g., Neilson et al., 2018), and require constant effort (e.g., Malpica-Cruz et al., 2016). Moreover, the possible movement of organisms as part of human-assisted migration to reduce the impact of climate change (see Chapter 4) brings with it the risk of unintentionally introducing other potentially invasive species, including non-native pathogens. The origin of disease outbreaks is difficult to determine, but for example, it has been argued that the epidemic that decimated the Caribbean keystone herbivore *Diadema antillarum* was due to a pathogen introduction via ballast water (Bak et al., 1984).

FUTURE GLOBAL CLIMATE PROJECTIONS

Global climate models provide the basis for future projections of coral health in response to climate change and the conditions that interventions will need to offset. The current suite of IPCC (Intergovernmental Panel on Climate Change) models (AR5) includes four emissions scenarios: a strong mitigation scenario (representative concentration pathway, or RCP, 2.6), two intermediate scenarios (RCP4.5 and 6.0), and a "worst-case" business-as-usual scenario

(RCP8.5). Global average surface temperature is projected to increase 2.6-4.8°C by 2100 under RCP8.5 and 0.3-1.7°C under RCP2.6 (Figure 1.4; Collins et al., 2013). Even if all emissions were curtailed today, an increase of 0.3-0.7°C is still expected to occur by 2035 due to "committed" warming driven by the long residence time of CO_2 in the atmosphere (Collins et al., 2013). While there are limitations in how these models are applied to predict corals' responses to climate change, they provide the best predictions of future SSTs. A fixed temperature-based threshold of 1-2°C above the historical summertime maximum is typically used in combination with future SSTs to predict bleaching (Donner et al., 2005; Frieler et al., 2013; Hoegh-Guldberg, 1999; Sheppard, 2003; van Hooidonk et al., 2013, 2014). The Degree Heating Week (DHW) cumulative stress index provides the basis for this empirically derived threshold (Strong et al., 2006).

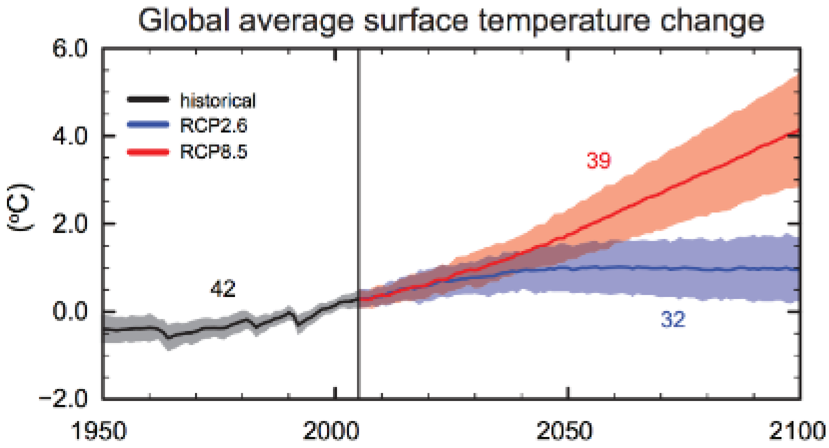

FIGURE 1.4 Change in global annual mean SST through 2100 relative to 1986–2005 based on the IPCC Fifth Assessment report. Shaded colors represent variability across multiple Global Circulation Models and Earth System Models for the worst-case emissions scenario (RCP8.5; red) and the strong mitigation (RCP2.6; blue) scenarios. SOURCE: IPPC, 2013.

Globally scaled models suggest that annual or biannual severe bleaching will occur by the 2050s under all emissions scenarios assuming no adaptation of corals (Figure 1.5; Donner et al., 2005; Frieler et al., 2013; van Hooidonk et al., 2013). This finding is similar to the earliest bleaching regional models applied to the Great Barrier Reef and Indian Ocean (Hoegh-Guldberg, 1999; Sheppard, 2003). To avoid this outcome, the majority of the world's coral reefs would require an adaptation rate of approximately 0.2-0.3°C per decade, with rates of up to 0.5-1.0°C per decade in certain regions (Donner et al., 2005). Recent studies have tested algorithms that explicitly account for historical thermal variability (Donner et al., 2011; Logan et al., 2012; Teneva et al., 2012) or incorporate specific mechanisms of adaptation and acclimation to rising temperatures (Baskett et al., 2009; Bay et al., 2017; Logan et al., 2014; Matz et al., 2018). These models generally find that even bleaching algorithms that include adaptive responses to warming predict corals only survive through 2100 under the lower emission scenarios (Bay and Palumbi, 2017).

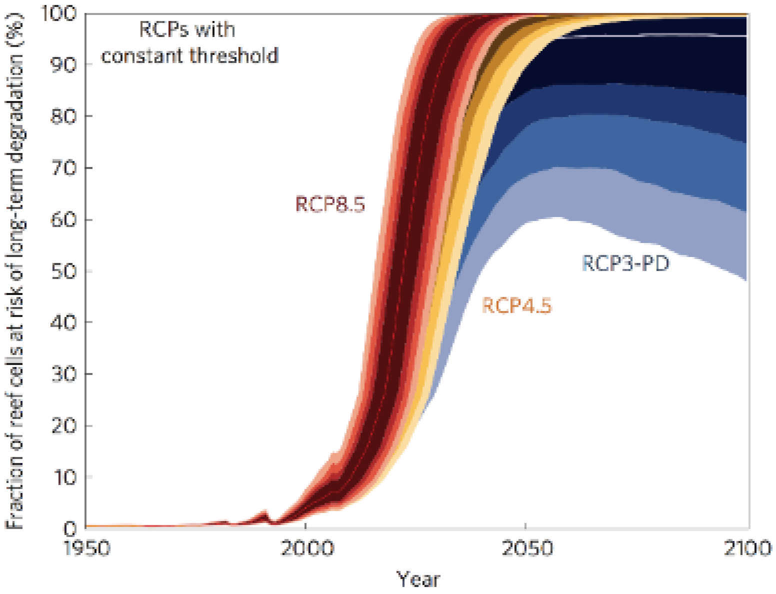

FIGURE 1.5 Assuming no increase in heat tolerance within species, projected probabilistic fraction of global coral reef cells expected to experience frequent severe bleaching events under IPCC AR5 emissions scenarios RCP8.5, RCP4.5, and RCP3-PD. Color gradations from light to dark indicate 95th, 90th, 84th, 75th and 50th percentiles. SOURCE: Frieler et al., 2013.

The effects of OA on future bleaching frequencies (Frieler et al., 2013; van Hooidonk et al., 2014), the consequences of rising SSTs on coral disease (Maynard et al., 2015), and the effects of sea level rise (Perry et al., 2018) have also been modeled at a global scale. While higher latitude areas may have a relatively lower frequency of future bleaching, corals in these “refugia” may encounter lower calcification rates driven by greater decreases in aragonite saturation state (Guionotte et al., 2013; Kleypas et al., 1999; van Hooidonk et al., 2014). Maynard et al. (2015) found that disease is as likely to result in coral mortality as bleaching in the next few decades. Perry et al. (2018) modeled expected reef accretion rates under projected sea level rise for tropical western Atlantic and Indian Ocean reefs and found that most reefs are expected to experience a mean water depth increases of more than 0.5 m by 2100 under RCP8.5. This change is projected to increase coastal flooding risk and change nearshore sediment dynamics. In addition to these global or multiocean basin forecasts, many regionally specific models have included coral communities with different thermal sensitivities, ecological interactions, evolutionary processes, and multiple stressors to predict future coral population sizes, extent of coral cover, and/or bleaching frequencies (e.g., Baskett et al., 2009; Anthony et al., 2011; Bay et al., 2017; Matz et al., 2018). Ongoing development of ecologically and evolutionary mechanistic models may better help predict how coral communities will change in the future.

Applying IPCC-based global circulation model (GCM) projections to predictions of coral distributions incurs inherent uncertainties at local and regional spatial scales and interannual and decadal timescales (Donner et al., 2005; Logan et al., 2014; Stock et al., 2011; van Hooidonk et al., 2014, 2016). However, near-term climate matching bleaching predictions may be more reliable using dynamically and statistically downscaled model projections for specific regions (e.g., Caribbean corals, van Hooidonk et al., 2015). Nevertheless, increases in thermal stress on coral reefs are presently so rapid at the global scale that using the next generation of GCMs are unlikely to change general bleaching projections (Donner et al., 2018).

STUDY TASK AND APPROACH

This study committee has been tasked with reviewing and summarizing the state of science on genetic, ecological, and environmental interventions meant to enhance the persistence and resilience of coral reefs. In this interim report, the committee provides a review and summary of currently available information on the range of interventions present in the scientific literature. As part of this review, the committee has been asked to evaluate the state of readiness of the interventions. To that end, the committee has attempted to identify the current feasibility, potential scale, risks, limitations, and infrastructure needs for implementation for each intervention. The committee did not prioritize or make recommendations regarding implementation of the interventions; the use of one or more interventions is a complex decision dependent on social, political, and environmental factors as well as the progress of future research. The committee's final report will build on this review to develop a science-based environmental risk assessment and decision framework to help inform actions to be taken by coral reef managers. As described in the committee's task, this report addresses item 1, with the remaining items to be covered in a subsequent report (Box 1.2). This study was requested and sponsored by the National Oceanic and Atmospheric Administration with additional support from Paul G. Allen Philanthropies.

This report is informed by a review of current literature and public information-gathering efforts. The committee acknowledges that this is a fast-moving field, and has made efforts to consider all currently available information, but due to new and upcoming research efforts, this may not be an exhaustive reference. Strong attention has been paid to similar efforts under way in other countries that are home to extensive reefs and strong research capacity, particularly in Australia. To explore this component of their task with the research and management community, the committee held workshops on May 31, 2018, in Miami, Florida and August 28, 2018, in Honolulu, Hawaii, and a virtual webinar on August 2, 2018. The agendas and panelists can be found in Appendix B. During these sessions, panelists discussed with the committee the risks, benefits, and feasibility of implementing novel interventions, as well as the underlying science driving their potential for effectiveness.

BOX 1.2
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.

Study Scope: Interventions that Increase Persistence and Resilience

The ability to resist or recover from disturbance, as well as the rate and pathway taken toward that recovery, are collectively termed resilience (Box 1.3). As a concept, resilience can be applied to different levels of ecosystems. Individual organisms can show physiological or growth resilience via survival, sustained growth, and/or reproduction (fitness), for example. Populations can show resilience through the ability to recruit new individuals after a disturbance. Communities can show resilience in ecosystem traits such as productivity, diversity, trophic linkages, or sustained biomass through shifts in species composition. A key goal for any intervention is that corals become more resilient in the field than they would have been without it. This goal is a scale issue as well—individual corals placed on reefs might be more resilient, but they might not be common enough to provide resilience to the reef itself or ecosystem services that the reef provides. This report is structured to address the interventions that have the potential to increase resilience at each of these scales. Additional measures are considered in this report that may increase the persistence of coral in deteriorating conditions, although they do not bestow resilience to the coral and in fact, by reducing exposure to stress, may hinder natural adaptation. However, they are important to consider as part of a toolkit of options for increasing coral survival.

While a focus on enhancing stress-tolerant genotypes or species is inherent to many of the interventions described in this report as a way to maintain overall coral cover, maintenance of diversity of genotypes or species is another consideration for supporting the goal of increasing resilience of coral reefs and their associated ecosystem services. Traditionally, the complex diversity of coral reef ecosystems has been described as being driven by a balance between natural disturbance from storms, competition, predation, and other stressors and recovery. Joseph Connell developed the classic idea that complex communities are at their most diverse at an intermediate level of disturbance (Connell, 1978), and he illustrated this in part with examples from coral reefs (Figure 1.6). Additional anthropogenic disturbance upsets this balance, often driving the community towards lower diversity, and affecting species in different ways than do natural disturbances. Yet, even in the face of human disturbance, reef corals and the ecosystem they create can recover. Such recovery occurs at the colony level when corals grow back from bleaching, at the population level when coral recruits settle in a disturbed area, and at the community level when disturbed species assemblages regenerate some ecosystem functioning.

BOX 1.3
Resilience

Resilience refers to the overall ability of individuals, populations, or communities to respond positively after disturbance, restoring some part of their original state. Resilience is often considered to have three major components. The first is *recovery*: the likelihood of and rate of an individual, population, or community returning to its original state after disturbance (e.g., bleaching or hurricane; Holling, 1973). A second component is *resistance*: the ability of an individual, population, or community to stay unchanged after disturbance (Holling, 1973; Levin and Lubchenco, 2008). A third concept is *reversibility*: the tendency of a community to shift back towards its original state rather than towards a different, but ecologically stable, alternative state. In some cases, a community can recover to its original state if the disturbance is small to moderate, but will shift to an alternate state (e.g., algae-dominated reefs) when the disturbance is strong. Therefore, a measure of ecological resilience is the basin of attraction, or distance to the unstable threshold, for the original (e.g., coral-dominated) state. Whether coral reefs exhibit alternative stable states is controversial (Mumby et al., 2013; Zychaluk et al., 2012), where the possibility of both coral-dominated and algal-dominated states being locally stable is likely most relevant under low herbivore density and diversity that would otherwise control algae dominance. Caribbean reefs exhibit greater evidence for alternative stable states than Indo-Pacific reefs (Roff and Mumby, 2012).

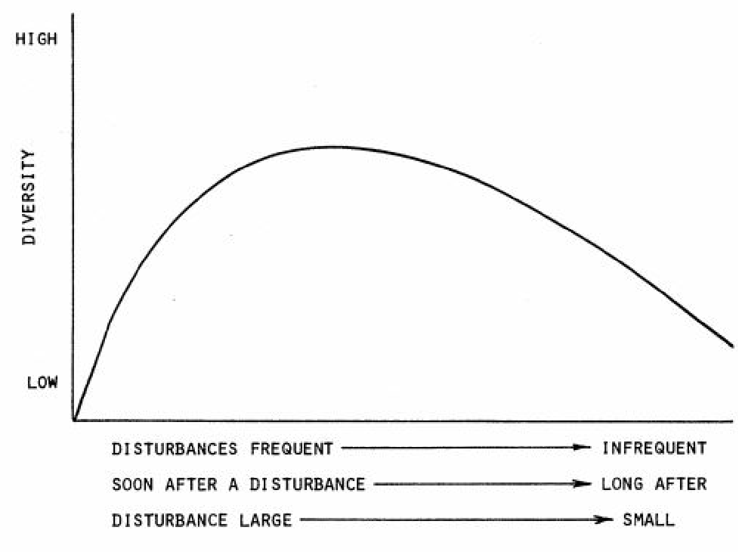

FIGURE 1.6 Figure developed by Connell (1978) proposing that low diversity occurs at high and low levels of disturbance. SOURCE: Connell, 1978.

Diversity can increase population-level adaptive capacity and community-level resilience to disturbance (Levin and Lubchenco, 2008). At the population level, greater genetic diversity leads to greater expected adaptive capacity to future stress such as temperature stress (Baskett et al., 2009). In addition, diversity might enhance reproductive success (Baums, 2008; Miller et al., 2018), which might be particularly important at high-stress conditions given the potential for stressors to reduce genetic diversity within populations of corals (Baums et al., 2013; Meyer et al., 2009). At the community level, diversity is an important attribute that determines the resilience and robustness of marine ecosystems, in addition to redundancy, modularity, and strong feedback loops (Levin and Lubchenco, 2008). For example, having a combination of slow-growing stress-tolerant species and fast-growing stress-susceptible species can theoretically increase the long-term likelihood of maintaining a coral-dominated state, especially under high disturbance levels (i.e., greater reversibility as defined in Box 1.3; Baskett et al., 2014). In addition to adaptive capacity or resilience to a single stressor such as thermal stress, having a diversity of genotypes or species might increase the likelihood of reef persistence when exposed to multiple stressors (e.g., disease, pollution, sedimentation, acidification, sea-level rise), especially under an uncertain future about the degree of change across stressors (Putnam and Gates, 2015) and uncertainty in the potential for tradeoffs in tolerance to different stressors. Furthermore, a diversity of corals and therefore reef structure might best support coral-associated assemblages (Graham et al., 2006; Gratwicke and Speight, 2005; Wilson et al., 2006) and full ecosystem function and services (Bellwood et al., 2004). Ultimately, the decision to focus on increasing the cover of tolerant genotypes or species and/or to focus on maintaining diversity will be driven by reef management goals and values at the local level. Similarly, whether these goals are accomplished regardless of species composition or whether native diversity is a priority to maintain is a choice that reef managers will make in selection and implementation of interventions.

This study focuses on interventions that improve the persistence and resilience of coral species to global stressors linked to climate change, particularly ocean warming and increased frequency of bleaching events, as well as ocean acidification. Disease prevalence is expected to be augmented by environmental stress, and also increases the vulnerability of coral to the stresses from changing climatic conditions; thus resilience to disease is also integral to this study. Mechanisms at the colony, population (e.g., increased recruitment), and community (e.g., support of species diversity) levels are considered. As directed by the statement of task, the committee does not emphasize management of local stressors. This is not because these stressors are unimportant, but rather because a great deal of attention and thought has already been paid to them, and control of these stressors is more manageable than control of global climate change.

Because corals are complex individuals with internal symbionts and a rich microbiome, we also review interventions that operate on these major features of coral biology. In particular, we consider interventions into the genetic makeup, the physiology, and the diversity of three different parts of the coral holobiome: the corals themselves, their algal symbionts, and the other members of their microbiome.

Aspects of environmental manipulation are included in the study for their potential ability to increase coral persistence by decreasing stress. Although these may not act on the resilience of the coral themselves, they may be an important tool in conserving reefs overall.

2

Genetic and Reproductive Interventions

The genetic information of an individual organism contains a blueprint for its response to a particular stimulus. Through natural selection, responses to the surrounding environment can cause the genetic composition of a population or species to change and shift. Coral reefs have existed for hundreds of millions of years, adapting and changing as the Earth's climate has changed (Veron, 2008). However, given the unprecedented losses in reefs caused by relatively fast changes in the Earth's climate over the last century, many coral populations may not have the capacity to adapt via selection at a sufficiently rapid rate (Bay et al., 2017). Genetic and reproductive interventions provide an opportunity to increase genetic diversity within populations to allow them to adapt to a changing environment, or permit selection of traits that may improve the resilience of coral populations and species. Coral reefs exist over a range of gradients, for temperatures and other stresses, from the reef scale up to variability across ocean basins. This indicates there is an ability for corals to acclimate or coral populations or species to select genotypes resilient to a range of conditions. Examining the genetic underpinnings of these adaptations is key to understanding and developing genetic interventions that could be employed to increase coral resilience and persistence.

Managed selection is a precursor to other interventions described in this report; it is an approach for identifying genetically resilient coral types. Observations of responses in the natural environment is one way to identify these corals, but a growing capability in molecular tools permits differentiation between evolutionary adaptations to a particular environment, as opposed to those individuals that are temporarily acclimated to change. The controlled and careful outcrossing of genetically distinct individual corals in a managed setting can be used to create a captive population with substantial genetic diversity. Individuals from captive propagation efforts can be released into the wild to increase the genetic diversity of native populations or by introducing resilient genotypes. There are several approaches that can be used to achieve these goals. Gamete and larval capture and seeding can improve coral reproductive success, and can also provide an opportunity for outcrossing of gametes with known beneficial genotypes. Coral cryopreservation adds the ability to preserve diversity in gametes or other stages until conditions improve and successful crosses can be made.

In the absence of naturally resilient corals, genetic manipulation may provide the opportunity to create resilient corals and coral symbionts. Discovery of the utility of CRISPR/Cas9 as a tool for creating gene drives, which create a biased system of inheritance for genes of interest, has driven interest in genetic manipulation. While CRISPR/Cas9 has been shown to be technically feasible to apply to coral, there is little knowledge regarding candidate genes upon which it could operate to increase resilience nor whether it may translate to a change in phenotypes. The ability to develop resilience in corals through gene drives is limited in the near term; however, genetic manipulation also provides an approach to experimentally identify the genetic causes of individual or species-level variation in stress tolerance.

MANAGED SELECTION

What It Is

Managed selection is the detection of corals with above average stress tolerance, and the use of them in subsequent interventions such as managed breeding, symbiont and microbiome isolation and manipulation, managed relocation, or genetic manipulation. Corals can thrive over a variety of environmental conditions, from the cooler waters of high-latitude reefs such as Hawaii, Bermuda, and Tonga to the warmer waters of equatorial islands, power plant effluents, and shallow patch reefs (Coles et al., 2018; Keshavmurthy et al., 2012). Their tolerances to a range of values for parameters such as temperature, salinity, sedimentation, light, and toxicant exposure reflect the ability of individuals to acclimate or populations and communities to adapt via selection of resilient phenotypes and species (Carpenter et al., 2008; Dixon et al., 2015; Jin et al., 2016; Palumbi et al., 2014; Rose et al., 2018).

Temperature is one of the parameters of greatest concern. Some habitats and locations have steady temperatures; for example, corals in fore-reef zones in Palau may normally experience a fairly narrow range of temperatures, from 26°- 30°C (Golbuu et al., 2007), while corals in Okinawa may be exposed to temperatures from 15°C - 30°C annually (Nadaoka et al., 2001), and those in the Persian/Arabian Gulf survive temperatures up to 36°C (Hume et al., 2013). However, other habitats even within these regions can show very different temperature patterns. For example, back reef, patch reef, or harbor environments may show higher daily temperature peaks (see Figure 2.1).

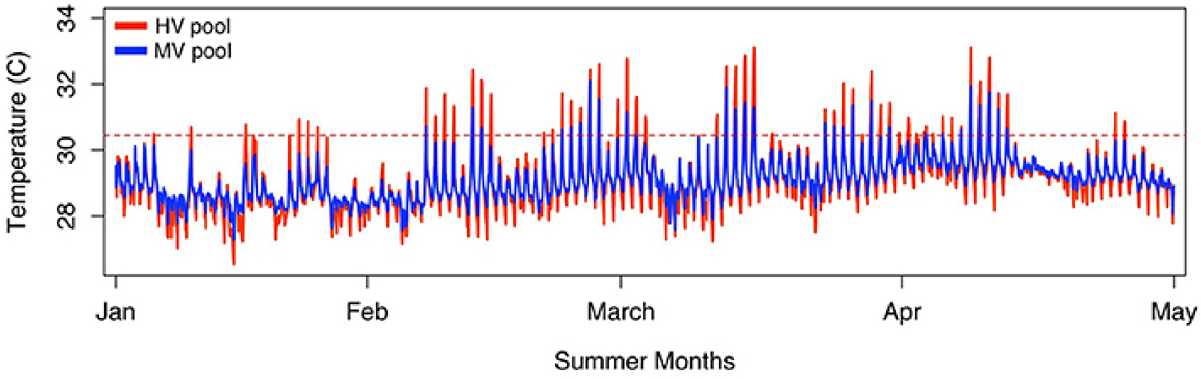

FIGURE 2.1 An example of short spatial scale temperature variation measured with recording thermometers on Ofu Island American Samoa. Temperature profiles of the highly variable back reef pool that houses heat-tolerant corals of several species (red) compared to the adjacent moderately variable back-reef pool where corals are less heat tolerant (blue). SOURCE: Thomas et al., 2018.

One set of coral species in Nikko Bay, Palau, persists in an environment typified by elevated seawater temperatures (32°C) and reduced pH (7.9), conditions which have been predicted to be common on reefs by the year 2050 (Anthony et al., 2011; Camp, et al., 2018). This bay has water retention and circulation patterns which models suggest retain coral larvae and gametes, and reduce immigration of propagules from reefs outside of the bay, suggesting the possibility of local adaptation in Nikko Bay to warm, acidic conditions (Camp et al., 2018; Golbuu et al., 2016; van Woesik et al., 2012). Other warm water habitats are embedded in the variable environmental mosaic of complex reefs at small spatial scales, and resident corals are not as isolated genetically. Overall, heat-related selection on reefs is associated with genetic differences occurring over the scale of hundreds of meters (Bay and Palumbi, 2015) or hundreds of kilometers (Dixon et al., 2015; Jin et al., 2016) at hundreds or thousands of gene loci.

Benefit and Goals

Managed selection takes advantage of the high level of genetic diversity found in many coral species, and the potential for natural selection to generate concentrations of adaptive alleles in habitats with high exposure to stressful conditions. In effect, it uses the long history of population adaptation across the environmental mosaic of the reef as a natural laboratory for the production of genetically adapted corals. Because this natural selection has been an ongoing process, adapted populations currently exist. As the raw material for subsequent use, corals chosen through managed selection are locally available, represent native coral genotypes, and can occur in large enough numbers to represent substantial genetic diversity for other traits. Because of these advantages, managed selection is currently a main target of operation for coral restoration before other more manipulative genetic interventions can be developed.

Another advantage is that conditions imposing multiple stresses on coral populations can currently be found. Corals with genotypes resistant to multiple stressors that often co-occur, such as higher levels of sediments and toxicants, with reduced light levels and salinities, occur near watershed discharge points have the advantage of tapping into the products of natural selection that may have taken place in habitats with multiple selective pressures. Rather than needing to perform controlled crosses and expend resources for grow out, these corals are already naturally available.

How to Do It

Corals that survive stress events or that are found in areas of known elevated stressor levels are obvious targets for studies of resistant genes and tolerances and may provide good source material for intervention activities. Examples of such sites for temperature stress include: (1) shallow back reef pools, reef flats, and patch reefs that heat up during daytime low tides; (2) lower latitude locations along latitudinally lengthy reefs such as the Great Barrier Reef or the Meso-American Reef; and (3) equatorial locations with high summer temperatures. There are also numerous other types of stressors for which geographic collections for resistance might be made: (1) harbors, for resistance to hydrocarbons and heavy metals (from fuel and antifouling paints); (2) offshore from agricultural sites for pesticides; and (3) locations adjacent to sewer outfalls for pharmaceuticals, nutrients, and low oxygen levels. Locations are typically assayed for stress levels (temperature, pH, and chemicals), sometimes at the scale of individual corals. Small portable, inexpensive temperature recorders have made it possible to measure temperature variation at small scales of space and time. Other stressors are more difficult and expensive to measure widely (Bahr et al., 2016; Kuffner, 2017)

A different source of information on stress tolerance is derived from monitoring the survival of individual colonies after major bleaching events. Seldom do bleaching events kill all the corals of a species on a particular reef (Depczynski et al., 2013; Glynn et al., 2001; McClanahan, 2004). Instead, there are often individuals that remain unbleached or that recover from bleaching.

Differential tolerance in corals to environmental stressors often has both a genetic component and an acclimation component (i.e., where an individual adjusts to an environment). Acclimation to stressful conditions is a widespread feature of coral populations (Bay and Palumbi, 2015; Coles and Jokiel, 1978; Jones and Berkelmens, 2010; Middlebrook et al., 2008) and as a result, phenotypic differences in corals collected from different reefs may not be entirely due to genetic or fixed features. Estimates of the amount of phenotypic variation in heat resistance due to acclimation have ranged around 50% in one study (Palumbi et al., 2014). Common garden experiments have been used to enhance the search for variation in stress tolerance that has a genetic basis in a wide variety of species (Parkinson et al., 2018).

Molecular tools can help identify the mechanisms and responses through which hardy corals survive stress, and eventually assist in identifying those corals most likely to survive in the future when used for active reef restoration. Genomics can be used to identify genotypic diversity associated with particular habitats and novel genotypes, providing targets for restoration outcomes. This approach is easiest when heat tolerance is associated with alleles of strong effect. However, most genetic analyses of heat tolerance suggest control by many genes. For example, offspring of corals from lower latitudes of the Great Barrier Reef show intermediate heat tolerance as if many genes were involved (Dixon et al., 2015). To date, the best model of heat tolerance is one controlled by alleles at many loci, each of which has small effect. Bay and Palumbi (2015) screened populations of *Acropora hyacinthus* and showed results suggesting hundreds of effective loci. Positive identification of these loci is challenging because of their small individual impact. Approaches based on genome-wide association studies, which rely on hundreds of thousands to millions of markers and sufficient sample sizes to detect marker-trait associations (Visscher et al., 2017), have provided a way to detect loci in wild populations (Barson et al., 2015; Lundregan et al., 2018), including those of smaller effect (Brieuc et al., 2015; Gagnaire and Gagiotti, 2016). Such studies also pave the way for identifying individuals that have high genomic breeding values for a trait—without knowing their actual marker-trait associations—using genomic prediction based on test populations (Crossa et al., 2017). This information in turn can be used to inform actions such as managed breeding and assisted gene flow (Flanagan et al., 2018).

Proteomics might also be used in a diagnostic manner to identify the key stressors at particular sites and the genotypes able to effectively respond through protein expression (Downs et al., 2005, 2012). Transcriptomics can be used to identify gene expression, which ties back to the genotypes exhibiting resistance and the effectiveness of the proteins being up- or down-regulated in response to specific stressors.

A few studies have been able to test the use of highly vetted stress-resistant colonies for controlled crosses and nursery grow-out (Guest et al., 2014) and to provide the raw material for candidate genes involved in stress resistance for future gene manipulation (Jin et al., 2016). A generalized procedure to identify genotypically stress-tolerant corals is to:

(1) Survey native populations across of range of stress levels for phenotypic variation in stress response;

(2) Move the highest- and lowest-resilience colonies to a common garden setting for further phenotyping after acclimation to common conditions;
(3) Characterize colony genomes, transcriptomes, and proteomes as well as symbiont types and microbial assemblages across a range of fixed stress tolerance; and
(4) Conduct manipulative experiments on roles of symbionts and microbes on colony tolerance.

Current Feasibility

The ability to monitor and identify stressed sites and collect corals from these locations is straightforward. The "omics" technologies of genomics (genetics), transcriptomics (gene presence and expression), proteomics (protein expression), and metabolomics (the study of metabolites and related processes) are already available for corals, and their applications are growing and improving rapidly (e.g., Aswani et al., 2015; Devlin-Durante and Baums, 2017; Downs et al., 2012; Miller et al., 2011; Ricaurte et al., 2016; Rougée et al., 2014). Identifying biomarkers for stress resistance of individual species has proven difficult (Parkinson et al., 2018), but individual phenotyping of corals after common gardening is currently feasible in marine laboratories with running seawater systems, corals transplanted into field conditions, or in coral husbandry businesses (e.g., Muller et al., 2018). Palumbi et al. (2014) have demonstrated fixed genetic differences and patterns of gene expression in corals over a range of temperatures, with both acclimatization and adaptation occurring within coral populations.

Protein expression studies in corals have proven particularly valuable in identifying cause-and-effect relationships between stressors and responses at the cellular level, prior to outright mortality (Downs et al., 2012). Specific classes of proteins such as xenobiotic metabolizing enzymes, including Cytochromes P-450 and multiple xenobiotic resistance protein, can be assayed both qualitatively and quantitatively to provide reliable data for identifying the contributions of individual stressors in a multistressor situation (Downs et al., 2005, 2012), supporting the design of specific and effective intervention strategies.

Potential Scale

The approach for finding "hardy corals" is broadly applicable across spatial, temporal, and taxonomic scales. Its scalability depends on how common stress-tolerant colonies are: if such corals are a rare discovery for a small number of species (e.g., Nikko Bay in Palau), the ability to use them broadly will be limited. By contrast, if they commonly occur on widespread coral habitats, such as patch reefs or back reef pools, and if these habitats house stress-tolerant corals of many species, then it may be possible to find multispecies heat-tolerant communities at many reef locations. The local availability of these corals would make their use in other interventions, including relocation and managed breeding, more feasible.

Risks

Broad scale tradeoffs are expected in the evolution of heat tolerance (Huey and Kingsolver, 1989). For example, polymorphisms in a population that confer the benefit of heat tolerance likely also confer some fitness disadvantage, otherwise they would be fixed by selection over time. The best-known example in corals is the tradeoff between the heat tolerance conferred by the symbiont genus *Durusdinium* (formerly *Symbiodinium* Clade D) and faster growth conferred by the heat-sensitive symbiont genus *Cladocopium* (formerly Clade C) (see Stat and Gates, 2011 for references and research history). However, recent experiments suggest that this tradeoff is less powerful in warmer waters (Cunning et al., 2015b). Other experiments have found tradeoffs between bleaching rate and disease (Shore-Maggio et al., 2018) in Hawaiian species, but Muller et al. (2018) found little relation in Caribbean staghorn corals. Tradeoffs between heat tolerance and colony growth or survival have also been harder to find; Kenkel et al. (2015) found evidence for higher transplant survival in Florida corals on native reefs but no tradeoff between heat tolerance and survival. Bay and Palumbi (2017) also found little tradeoff in growth among heat-resistant corals but suggested that strong selection for heat tolerance also selected for high transplant survival.

Risks of performing “omics” analysis on corals include further damage to corals that survive bleaching events, collecting pressure on corals in stress-tolerant populations, and mis-assignment of phenotypic variation in common garden experiments as genetic rather than epigenetic. Additionally, there are risks to the various interventions that may make use of selected coral genotypes, such as managed breeding or relocation, described later in this report.

Limitations

A limit to this approach might be encountered if these naturally-growing stress-tolerant corals cannot tolerate extreme stresses expected under reasonable climate models at the end of this century. For example, if currently available natural tolerance provides 2-3°C extra resilience against heat pulses, but 4-5°C is expected under high CO_2 emission scenarios, then currently available stress tolerance may not suffice. Experiments in artificial selection classically show that phenotypic change from generation to generation slows after initial increases, even for genes under control of many additive loci. There are currently few ways of confidently predicting exactly where this asymptote will be for any coral species. In such cases, use of natural variants can be expected to extend the lifetime of current reefs, and provide raw genetic material to generate extreme stress tolerance in the future through breeding or manipulation. But natural variants alone may not suffice to generate heat tolerance needed in all future scenarios.

Infrastructure

The approach described above suggests that facilities to collect and maintain corals are required, as is equipment to monitor stress levels of local habitats. Specialized laboratory equipment is needed for the genomic, proteomic, and transcriptomic analyses.

MANAGED BREEDING

What It Is

The restoration of reefs through artificial propagation has increasingly found traction over the past decade (Hesley et al., 2017; Lirman and Schopmeyer, 2016; Rinkevich, 2014). Many such activities are focused on "coral gardening," the propagation of coral fragments in nurseries, and their outplanting on degraded reefs. These low-cost and readily adaptable approaches may have some associated risks such as disease transmission and changes in wild population genetic diversity. However, there are examples of long-term survivorship, growth and reproduction (Lirman and Schopmeyer, 2016), and retention of genetic diversity (Drury et al., 2016) at several restoration sites. The development of infrastructures that support the culture and restoration of corals has paved the way for the development of additional approaches based on sexual reproduction—managed breeding. These approaches range from supportive breeding within populations to hybridization between populations or species.

Managed breeding relies on the outcrossing of genetically distinct individuals, regardless of their taxonomic status. This chapter encompasses three approaches under this category that support varying goals in restoration, from increasing coral cover while preserving local genetic diversity, to increasing cover by introducing individuals with novel genotypes and higher fitness. *Supportive breeding* seeks to enhance population size by sampling a subset of individuals from a population for captive rearing, and then releasing the captively reared offspring back into their native habitat (Ryman and Laikre, 1991). *Outcrossing between populations* aims to introduce novel genetic variation within a species range, following reproduction between individuals from different populations. *Hybridization between species* is the use of sexual reproduction to create individuals with novel genotypes that are more fit than the parental species.

Benefit and Goals

Interbreeding between individuals can have positive and negative outcomes. To place these outcomes in perspective, it is helpful to view populations and species as belonging to a breeding system continuum (Figure 2.2), where optimal effects of outcrossing are intermediate to fitness losses due to inbreeding or outbreeding depression (Allendorf and Waples, 1996; Edmands, 2007). These continua are likely to be taxon specific. Activities associated with managed breeding might be targeted at different degrees of outcrossing.

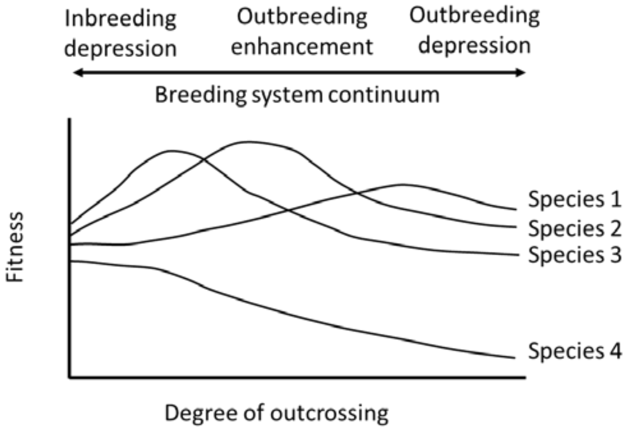

FIGURE 2.2 Breeding system continuum, describing theoretical fitness outcomes of outcrossing. SOURCE: Modified from Allendorf and Waples, 1996 with information from Edmands, 2007.

Supportive breeding within populations seeks to increase population sizes and local genetic diversity, thus improving long-term persistence. Therefore, this intervention supports recovery goals that aim to improve coral cover while maintaining genetic variation within native species.

In corals, supportive breeding may provide benefits both through captive rearing and through the release of artificially propagated individuals. Captive rearing provides a means of retaining genotypes that may be otherwise lost in wild populations (Schopmeyer et al., 2012), and can also increase genetic diversity within populations through sexual reproduction. Outplanting locally derived captive reared corals on degraded reefs may provide demographic support by augmenting wild population sizes (Ryman and Laikre, 1991). This outcome may be accompanied by an increase of genetic diversity and effective population size. An augmented population would have an increased ability to adapt to a changing environment because selection is more efficient in large populations (Falconer and Mackay, 1996; Kimura, 1983). Supportive breeding can be expected to assist population recovery if reintroduction success is high. The manipulation of gene flow can result in scenarios with beneficial outcomes, depending on the degree of domestication selection in captivity (Baskett and Waples, 2013; Ford, 2002). Supportive breeding has significant potential to address problems with low recruitment in the Caribbean (Kuffner and Toth 2016; van Woesik et al. 2014).

Outcrossing between populations aims to increase fitness within populations, and hence population size, by introducing additional genetic variation from other populations through reproduction and gene flow. This intervention can also be used to meet recovery goals directed at increasing coral cover.

In certain scenarios, outcrossing may result in increased fitness in offspring compared to the parents (Figure 2.2). Such an increase, or heterosis, is attributed to the masking of deleterious alleles or to greater fitness in heterozygotes compared to homozygotes. Immigrants into a small population can result in genetic rescue—an increase in population fitness due to the introduction of new alleles (Tallmon et al., 2004; Whiteley et al., 2015). For genetic rescue to occur, the offspring of immigrants would need to elevate the overall fitness of the target population, ideally accompanied with an increase in population size. The benefit of this approach is the recovery of small and fragmented populations with limited ability to adapt to a changing environment. If persistent gene flow occurs between fragmented subpopulations, the overall effective population size of the metapopulation may be increased as a whole, thus reducing the likelihood of inbreeding, and minimizing divergence. Genetic rescue has been implemented in a small number of examples; its utility may be underappreciated in population recovery (Frankham, 2015; Whiteley et al., 2015). Relevant data on the potential for outcrossing between coral populations is limited; although self-fertilization and inbreeding in corals have been well documented (Baums, 2008), inbreeding depression has not (Baums et al., 2010). The potential for fitness improvements due to heterosis is untested in corals. However, genetic load is generally high in marine invertebrates (Plough, 2016), suggesting the potential for this intervention.

Hybridization across species aims to create novel genotypes that are more fit than the parental species that were used to create the hybrids. The use of hybrids in coral reef recovery may vary. If the goal is to increase coral cover while reducing impacts on local species diversity, then infertile hybrids may be preferred. If the goal is to increase cover and the long-term fitness of a community using individuals with novel genotypes, fertile hybrids may be preferred.

Outcrossing between species immediately creates novel genetic variation within a hybrid taxon and provides additional material for mutation, drift, and selection to act upon. These processes can result in diversification and new adaptations and have played a key evolutionary role in species evolution across taxa, including corals (Richards and Hobbs, 2015; Vollmer and Palumbi, 2002; Willis et al., 2006). The potential benefit of human-mediated hybridization between species would be the development of new forms that have higher fitness than the progenitor species, which may also provide the basis for future selective breeding programs. Although typically avoided in conservation efforts, there have been increasing calls for the use of interspecific hybridization in the face of rapidly changing environments (Hamilton and Miller, 2016), because they may provide adaptive potential beyond that of the phenotypic range of the parental species and a means of preserving genomes at the risk of extinction.

How to Do It

The identification of target populations and species is a crucial first step, and depends on location and local reef restoration goals. Practically, managed breeding relies on many of the same practices for propagation of coral fragments in nurseries and their outplanting that have been developed for traditional restoration projects, some of which are described in Box 2.1.

Supportive breeding within populations would rely on species that can be readily propagated using sexual reproduction, have a high reintroduction success, and would significantly contribute to reef building. Fitness outcomes associated with supportive breeding and restoration have been extensively studied in many marine species (Bell et al., 2005; Blaxter, 2000; Hedgecock and Coykendall, 2007; Naish et al., 2008; Waples et al., 2012), and best practices based on available science have been proposed (Waples et al., 2012). Briefly, development of an effective program relies on the maintenance of diverse populations, clear program objectives, clearly outlined broodstock management and release protocols, and long-term monitoring of enhanced populations. The use of wild-derived individuals as broodstock for the captive population in every generation of supplementation is aimed at preventing divergence between the two and relies on processes in the natural environment to drive the ongoing evolution of the population as a whole. “Integration” of captive-reared and wild populations has gained considerable traction in the conservation of some species such as salmonids and shellfish (Waples et al., 2012). Several empirical examples support the potential use of wild broodstock in retaining genetic diversity over the short term (Ford et al., 2016; Hess et al., 2012; Waters et al., 2015, 2018), but others indicate reduced fitness in captive-reared individuals compared to wild conspecifics (Christie et al., 2014). In corals, inadvertent selection due to domestication may occur through several mechanisms, because these species have high fecundity, high variance in reproductive success and high mortality at settlement. Therefore, such studies provide insight into the importance of developing appropriate protocols for broodstock collection, and rearing and release strategies.

Outcrossing between populations requires prior knowledge of the fitness of individuals resulting from such crosses within the environment of the reef to be restored. Such efforts may also need to account for any future environmental changes in the target populations.

Characterization of the extent of local adaptation and population structure across a species and identification of management units would provide additional information to support these endeavors. Feasibility studies on the number of individuals needed can be based on tests using laboratory studies or outplanting small numbers of crosses within the target reefs (Whiteley et al., 2015). Ideally, such tests should use more than one generation of outcrossing, and include different cross types, such as second-generation (F2) crosses and backcrosses to individuals representing the native populations.

Hybridization between species would rely on candidate species that provide viable offspring following reproduction and would use similarly well-developed protocols for within-species crosses, although the evaluation of risks to existing natural populations would likely differ. Since the intent would be to create new forms that have higher fitness than the progenitor taxa, initial field testing of hybrid performance in different target environments is essential. Testing of hybrid fertility is essential for risk assessment. In some cases, infertile hybrids may be desired simply for their potential to return habitat to a degraded reef. On the other hand, fertile hybrids may provide an opportunity to create new genotypes that are more capable of adapting to a changing environment. Determining the long-term consequences of hybrids over several generations is important to understand in this context, because in some cases fitness benefits in first-generation (F1) hybrids decrease or disappear in future generations (Burton, 1990).

BOX 2.1
Cultivation and Outplanting

Many interventions described in this report ultimately will rely on techniques to cultivate selected or manipulated coral propagules and introduce them to the environment through larval seeding or outplanting. Coral propagules for cultivation can be made via colony fragmentation, polyp excision, collection of brooded planula larvae upon their release, and through the collection of gametes from spawning species (Harrison, 2011). Fragmentation and excision provide new individuals genetically identical to the parent stock, while sexually produced planula larvae allow for additional genetic variation and selection/crossing for particular traits (Richmond et al., 2018). Numerous facilities are producing material for reef restoration efforts and outplanting.

Cultivating fragments entails a variety of techniques in land-based facilities and in the ocean. Fragments can be attached to blocks resting on the ocean bottom, in trays, or suspended in mid-water from structures (Barton et al., 2017). Adhesives include underwater epoxy, super glue, or mixtures of cement and Plaster of Paris (Dizon et al., 2008). A technique called microfragmentation accelerates the growth rates of massive and encrusting species, as small pieces of genetically identical coral will grow quickly and fuse when in contact with each other (Forsman et al., 2015b). Culture success can further increase with reduction in overgrowth by algae through addition of herbivores such as sea urchins (e.g., Serafy et al., 2013). Because species and clones within species often have such different responses to fragmentation and replanting (Morikawa and Palumbi, in press), it is generally good practice to maintain records of the response of clones. Such records benefit from accurate, rapid, and inexpensive genotyping within species, an area of active research and technique development (Kitchen et al., 2018).

Cultivating planula larvae is less well-developed than fragmentation largely because of the low availability of gametes in most corals except during annual spawning. Recent advances in captive coral cultivation include successful production of planula larvae from controlled crosses and stock material for transplantation into the field (Chamberland et al., 2015, 2016, 2017; Guest et al., 2010; Omori et al., 2003). Gametes can be collected from coral colonies reared under experimental conditions to produce them numerous times a year, and research is under way on selection for specific traits including higher temperature tolerance (Pollock et al., 2017b). If such research is successful in identifying and breeding for such traits, asexual processes can replicate these genotypes for transplantation into the field or to other facilities for additional grow-out. Recent efforts in the Caribbean, Atlantic, and Pacific have demonstrated it is possible for coral larvae to be successfully reared *ex situ* (Lirman and Schopmeyer, 2016) and outplanted on artificial substrate (Chamberland et al., 2017), but the capacity for successful outplanting of such larvae at ecologically-relevant scales remains unproven.

Coral are introduced or restored to an environment through reattachment to reef surfaces. Colonies can be fixed to reef surfaces with a variety of adhesives, ties, and in a variety of species configurations and densities. Little research has been done on ideal methods to accelerate growth and survival in natural settings, but these are likely to be location and species specific. If the corals are being relocated to a new place where a reef structure does not currently exist, artificial structure would need to be created to allow attachment of translocated corals. If larvae are being introduced, settlement rates may be increased with addition of settlement-inducing cues, such as addition of a ground mixture of crustose coralline algae (Pollock et al., 2017b).

One consideration in the final attachment step is the number of fragments to transplant. A greater number of transplants might increase the likelihood of transplant success through more replicates. However, this also increases the potential to overwhelm local populations and naturally-occurring acclimatization, adaptation, and range shifts, especially given uncertainty in when and where to move stress-tolerant individuals (although this is only likely for very small populations; Matz et al., 2018). If transplantation is occurring to a location with degraded or nonexistent reef structure, then transplanting sufficient numbers and diversity beyond demographic and genetic Allee effect thresholds might be necessary (Baums, 2008).

Fragment survival can range from low (50-100% mortality in the first 5 years) to high (>70% survival; Young et al., 2012), and settlement rates for introduced larvae can likewise be quite variable, ranging from <10% to 90% (Guest et al., 2014; Pollock et al., 2017b). Recruitment requires appropriate substrata with the right metamorphic inducers (e.g., CCA and bacteria). To enhance the likelihood of survival, reproduction, and recruitment, management of local stressors such as clearing of macroalgae, turfs, and sediments as well as removal of corallivorous snails and fireworms will be important (Young et al., 2012). In addition, placement in more wave-sheltered locations within the larger target area can reduce the likelihood of mortality from storms, a significant source of post-outplanting mortality. Further, reintroduction of herbivores such as the urchin *Diadema antillarum*, either through relocation (Maciá et al., 2007) or culturing (Williams, 2016), can increase coral survival and reproductive success by increasing the grazing on algal competitors (Idjadi et al., 2010), though overgrazing may damage recruits (Davies et al., 2013).

Current Feasibility

Supportive breeding within populations relies on the propagation of corals using sexual over asexual methods, and success is dependent on high survivorship after reintroduction and demonstrated recruitment following outplanting (Box 2.1). Sexual reproduction of captive broodstock has been successful in a number of species, including *Acropora tenuis* (dela Cruz and Harrison, 2017; Nakamura et al., 2011; Omori, 2011), *A.valida* (Villanueva et al., 2012), *A. millepora* (Guest et al., 2014), and *A.digitifera* (Edwards et al., 2015).

While systematic efforts at supportive breeding of coral have not been established, investigations of different release strategies of captive reared individuals point toward possible strategies that might be implemented more broadly. Efforts to date have largely focused on single generation releases, have occurred on a small scale, and have relied on local broodstock (dela Cruz and Harrison, 2017; Guest et al., 2014; Nakamura et al., 2011; Villanueva et al., 2012). Mass releases of larvae adjacent to healthy coral ecosystems in Palau were reported to have limited success post-settlement, possibly due to competition with natural recruits (Edwards et al., 2015). In contrast, larval seeding (described further in the Gamete and Larval Capture and Seeding section) in degraded areas in the northwest Philippines resulted in enhanced recruitment and increased coral cover after 3 years (dela Cruz and Harrison, 2017). Reintroduction of juveniles, rather than larvae, has potential to reduce losses due to early mortality (Nakamura et al., 2011). Given that research in this area is relatively new, most studies examined success rates within a single generation; however, natural reproduction in recruits has been reported in both larval seeding efforts (dela Cruz and Harrison, 2017) and juvenile outplanting (Guest et al., 2014). Organizations such as SECORE International are currently investigating a range of outplanting approaches with sexually produced offspring. Sexual reproduction has also been observed following outplants of nursery-grown fragments (Carne and Baums, 2016).

These initial studies indicate that approaches based on sexual reproduction of captive broodstock and release of offspring are feasible and point toward their potential in larger programs. The long-term success of supportive breeding programs over several generations has yet to be realized.

The infrastructure and protocols for **outcrosses between populations** would rely on those developed for supportive breeding, and therefore are technically feasible. In addition, research on transporting corals over long distances and inducing synchronous spawning has been demonstrated in some species (Craggs et al., 2017, 2018). There are few systematic efforts at investigating the fitness of within-species hybrids at different levels of divergence. However, Dixon et al. (2015) demonstrated the potential for introducing novel genetic variation into a cold thermal tolerant population of *A. millepora* following experimental crosses with a warm tolerant population, which in turn permitted a rapid response to heat selection within the newly created population. Additional information on population structure (Baums, 2008; Chiazzari et al., 2013; Flot et al., 2011; Forsman et al., 2015a, 2017; Suzuki and Fukami, 2012; Toonen et al., 2011) and local adaptation in coral species (Baums et al., 2014; Pratlong et al., 2015; Sanford and Kelly, 2011), suggests that additional experimental investigations of hybrid fitness within species are feasible. Such investigations would need to carefully consider genotype-by-environment interactions in field testing (Drury et al., 2017; Dubé et al., 2017).

Direct investigation of the use of **hybridization between species** in coral habitat recovery is in its infancy, but several studies provide support for ongoing research. The creation of novel variation through interspecific hybridization depends on the ability to create fertile hybrids, increased hybrid fitness compared to the progenitor species, and maintenance of fitness gains across generations. There is substantial evidence that natural hybridization has played a historic role in the evolution of several coral taxa (Arrigoni et al., 2016; Budd and Pandolfi, 2010; Combosch and Vollmer, 2015; Richards and Hobbs, 2015; Willis et al., 2006), suggesting its possible role in restoring fitness as part of a deliberate intervention. Furthermore, contemporary hybridization may play an ongoing role in adaptation. For example, population declines of two *Acropora* species (*A. cervicornis* and *A. palmata*) in the Caribbean have been accompanied with increased incidence of their F1 hybrid *A. prolifera* (Fogarty, 2012). Such patterns may be especially relevant to environments that are peripheral to the species range (Budd and Pandolfi, 2010; Fogarty, 2012; Hellberg et al., 2016) that may represent near-future climate scenarios.

The ability to create viable hybrids in artificial environments varies across genera that have been studied. Hybrids between species within *Ctenactis* were not viable (Baird et al., 2013), whereas experimental hybrids belonging to *Montipora* and *Platygyra* were (Willis et al., 1997). Many species belonging to the genus *Acropora* exhibit limited pre- and postzygotic isolating mechanisms (Baird et al., 2013; Fogarty et al., 2012a, 2012b; Isomura et al., 2016; Willis et al., 1997), and thus serve as candidates for the investigation of fitness in interspecific crosses between species representing a range of divergences.

Few studies have directly investigated hybrid fitness relative to parental species. Most reports are from the genus *Acropora*. In the Caribbean, hybridization involves the only two species in the region, *A. cervicornis* and *A. palmate,* where F1 hybrids between the two had comparable fitness with the parental species across life history stages measured (larval survival, post-settlement survival) and higher settlement and growth rates in shallow environments (Fogarty, 2012). In the Indo-Pacific, the survival of juvenile *A. millepora* × *A. pulchra* F1 hybrids outplanted in three habitats in the Great Barrier Reef varied, with growth and survival comparable to or exceeding the nonlocal parent species (Willis et al., 2006). In the most comprehensive study to date to directly investigate the potential for hybridization in reef restoration, W. Y. Chan et al. (2018) examined the relative fitness of hybrids and their progenitor species, using two more divergent (*A. tenius* and *A. loripes*) and two more closely related (*A. sarmentosa* and *A. florida*) cross types (five colonies per species). Survival to 28 weeks, size at 28 weeks and 1 year, photochemical efficiency, and algal symbiont uptake were measured in F1 offspring raised in ambient and elevated temperature and pCO_2 environments. Generally, no significant difference between hybrid and parental performance was detected across a number of traits, and all cross types had lower size and survival in the elevated environment. However, *A. sarmentosai* x *A. florida* hybrids had higher survival and growth rates than the parental species under ambient conditions. There was also some support for the role of hybrids under changing conditions. In the elevated environment, *A. tenius x A. loripes* hybrid survival was greater than *A. tenius*, and photochemical efficiency was higher than both parental species. Hybrids representing one cross direction (female *A. florida* x male *A. sarmentosai*) had higher survival than one parental species under elevated conditions. Taken together, the results of these studies indicate that there may be circumstances under which F1 hybrid *Acropora* might perform better in some environments.

Research in this area would benefit from systematic investigation of different cross types across a range of species divergences, increases in sample sizes, and performance testing across a variety of environments. Since research on hybrid viability is recent, the fitness consequences of interspecific hybridization beyond the F1 have yet to be directly studied. However, it appears that *A. prolifera* may be able to reproduce with at least one progenitor species in the natural environment, because there is evidence of unidirectional gene flow from *A. palmata* into *A. cervicornis* (Vollmer and Palumbi, 2002, 2007). There are also challenges in extrapolating these findings to other coral reef species.

Potential Scale

In corals, **supportive breeding within populations** has typically targeted individual reefs using few species. **Outcrossing between populations** and **hybridization between species** has been conducted within laboratory settings only. In all cases, successful introduction of captive-bred individuals would benefit corals on the reef-scale, if they are able to increase coral cover. Long-term fitness benefits and persistence of populations would be dependent on connectivity within the reef in cases where sexual reproduction and self-recruitment are desired.

Currently, supportive breeding programs based on larval releases or juvenile outplanting have been conducted as single experimental events. Ideally, populations should become self-sustaining after a limited-time captive breeding and release program; however, in other taxa, population rebuilding has involved ongoing captive propagation and release, often for decades (Laikre et al. 2010; Naish et al. 2008). Published literature has reported the outcomes of single generation crosses both with and between species. However, if restoration goals are dependent on ongoing sexual reproduction, multigenerational studies are needed, because reductions in fitness may only be observed beyond the F1. If goals rely on sterile individuals, then fertility in hybrids would need to be investigated.

Risks

Outcrossing may result in fitness reductions, depending on the scenario (Figure 2.2). Outbreeding depression is ascribed to two mechanisms: loss of local adaptation (extrinsic outbreeding depression) or disruption of co-adapted gene complexes (intrinsic outbreeding depression) (Templeton, 1986). In the former, individuals created as a result of outcrossing or hybridization receive only half the allelic combinations present in either parent population, and may be unsuited to one or both of the parental environments. In the latter, recombination between different parental genomes may lead to a breakdown of interactions between co-adapted loci that are inherited together and influence a fitness trait. Decrease in fitness might be observed as early as the first generation of crossing, but it may be delayed until recombination in subsequent hybrid or backcrossed generations. Outbreeding depression is predicted to be prolonged for a greater period if intrinsic mechanisms are involved: selection is more likely to be effective in restoring favorable alleles following the loss of local adaptation than after the disruption of co-adapted loci (Edmands and Timmerman, 2003). Persistent gene flow between evolutionary divergent populations can result in loss of population structure and locally adaptive traits if hybrids are less fit, which could degrade the total genetic variation across the entire metapopulation (Spichtig and Kawecki, 2004).

Ongoing outcrossing or gene flow may also affect the demographic properties of a population (Allendorf et al., 2001). In scenarios where outcrossing benefits population fitness as a whole, population sizes might increase because effects such as genetic drift, inbreeding depression, and reduced adaptability will diminish. In contrast, outcrossing that leads to reduced fitness can result in the opposite outcomes. Population losses can also accrue following reproduction between less fit hybrids and the parental species, if the former occur at higher frequencies (Allendorf et al., 2001; Ronce and Kirkpatrick, 2001).

Genetic risks due to human-mediated outcrossing and hybridization have been extensively documented in marine species (Waples et al., 2012). Most information comes from species that depend on sexual reproduction exclusively and are shorter lived. Generally, the risks involved depend on the program goals, and on the accepted level of impact that captive-reared individuals have on wild populations. In all cases, risks should be evaluated with the development of genetic management plans that include clear performance indicators and monitoring plans.

The goals of **supportive breeding within populations** are usually aimed at increasing population sizes and recruitment rates while maintaining or restoring the genetic diversity and fitness of a target wild population (although evidence of erosion of genetic diversity in coral populations is currently minimal; van Oppen et al., 2015b). Maintaining a broad range of genotypes within a population facilitates its adaptation to a future unpredictable environment. Managing the risks depend on the ability of the rearing program to sample sufficient diversity from wild populations, retain that genetic diversity through the captive rearing programs, prevent adaptation to culture conditions, maintain an optimal effective population size in the reintroduced individuals, and ensure a high reintroduction success. Loss of genetic diversity in wild populations can occur if offspring contributions from few captive-reared families dominate (Hedgecock and Coykendall, 2007; Ryman and Laikre, 1991). Corals species are highly fertile, but with variation in reproductive success. Self-incompatibility, as well as incompatibility between genotypes has been reported (Miller et al. 2018), which means that captive rearing may result in the release of many individuals representing few families. Such releases can result in genetic homogenization, which in turn limits responses to environmental changes. Loss of fitness due to captive rearing and release can also occur through inadvertent selection. For example, high variance in reproductive success, and large nonrandom mortalities in larvae or juveniles can result in fitness losses. In a review of 266 studies on the genetic effects of captive-rearing programs, including marine invertebrates, significant losses in fitness were reported in about half of studies relative to wild populations (Araki and Schmid, 2010).

Generally, genetic effects of captive rearing can be reduced by collecting wild broodstock for every generation of culture and by moderating release sizes (Waples et al., 2012). Therefore, supportive breeding in corals can take advantage of the fact that gametes can be collected from the wild for each captive-reared cohort (Box 2.1). In this case, it is important that divergent wild source broodstock be maintained in the natural environment.

The goals of **outcrossing between populations** are theoretically aimed at increasing the fitness of a wild population. Success depends on knowledge of the extent of population structure and local adaptation, and the fitness outcomes of hybridization beyond the first generation.

Guidelines have been proposed for predicting the risk of outbreeding depression in the absence of species-specific information (Frankham et al., 2011). The risks associated with captive rearing are similar to those of supportive breeding. Additional risks are associated with demographic losses to both the donor and recipient populations, due to decreased fitness in the offspring of crosses, especially following reproduction with native populations. However, in some coral populations, there may be few colonies that support natural reproduction and recruitment (Kuffner and Toth, 2016); therefore, the use of crosses between-population for coral rebuilding may outweigh concerns associated with possible fitness losses.

The genetic risks of **hybridization between species** would vary with hybrid fertility. If fertile hybrids are desired for restoration goals, risks similarly depend on the likelihood of outbreeding depression, especially over several generations. The creation of hybrids might itself result in loss of genetic diversity through a bottleneck, caused either by the use of few individuals in initial crosses, or through the production of a wide range of novel genotypes that include less fit individuals. This bottleneck may influence genetic diversity in subsequent generations. Introduction of fertile hybrids within the same range as the parental species might result in demographic losses to the latter, through reproduction. If hybrids are infertile, then losses to the parental species within the introduction range will be minimal. However, both fertile and infertile hybrids might also compete with native species. Both genetic and ecological risks would be affected on the ability to create and outplant sufficient numbers of hybrid individuals. Ecological effects such as competition may be small in situations where there is substantial degradation of the coral reef. Hybrids between native and invasive species have caused diversity declines within and among populations in a number of cases (e.g., Fitzpatrick and Shaffer, 2007; Hitt et al., 2003; Mooney and Cleland, 2001; Neira et al., 2006; Rhymer and Simberloff, 1996).

Limitations

All forms of managed breeding rely on the identification of suitable target species and populations. Within the Caribbean, there are five to seven main reef-building species (e.g., Gladfelter et al., 1978), but within the Pacific there are many more (e.g., deVantier et al., 2006). All approaches rely on a sufficient supply of broodstock so that founder events are avoided in the captive populations and available genotypes are well represented. Since asexual reproduction may be relied upon for the development of broodstock collections in coral species, this limitation may be readily addressed. On the other hand, asynchronous spawning between individuals may lead to a reduction in fertilization success or underrepresentation of specific cross types (e.g., Craggs et al., 2017; Miller et al., 2018). This issue may be especially problematic for the development of within- and between-species crosses. Culturing relies on adequate rearing spaces to prevent loss of genetic diversity. Releases should result in sufficient numbers of individuals representing a broad array of genotypes. Recommendations for sufficient population sizes at all stages of culture vary by species (Waples et al., 2012). Goals are aimed at maximizing the effective population size while balancing realistic limitations imposed by the biology of the species, at maintaining diverse genotypes in coral culture, and at maximizing recruitment rates in the wild after release. Measuring program success by tracking the long-term fitness and reproductive success of outplants is essential, and may be challenging in scenarios where released individuals cannot be tagged. In corals, larval releases may be tracked using approaches such as age-dependent cohort analyses or by genetic-based markers if the latter are sufficiently powerful. Outplanted corals settled on substrates may be readily tracked over time.

Supportive breeding within populations relies on sexual reproduction, but asexual reproduction is known to be dominant on many reefs in the Caribbean (Miller et al., 2018), particularly those dominated by branching species (Kuffner and Toth, 2016). Within broadcast spawners in the Caribbean, many genotypes are known to be incompatible (Baums et al., 2013), but multi-genet crosses have resulted in high genetic diversity (Miller et al., 2018). There is some concern that putative broodstock sources are dependent on older, senescent colonies that have either lower viability, or are no longer adapted to prevailing or changing environmental conditions (Devlin-Durante et al., 2016; Irwin et al., 2017).

Both **outcrossing between populations** and **hybridization between species** depends on adequate field-testing. Such testing should occur over more than one generation, since there are concerns about reduced fitness over more than one generation. However, depending on the growth and lifetime of the F1 generation, they may provide sufficient reef structure to support conservation goals. There is evidence that predictors for performance such as growth rate may not be sufficient over the lifetime of colonies (Edmunds, 2017) and that laboratory-based studies may not adequately predict field success (O'Donnell et al., 2018). Hybrid performance is likely to vary between field sites, and it is possible that a wide range of cross types would have to be examined for their contribution to reef building.

Infrastructure

Infrastructure for managed breeding is largely needed for the selection of propagules from the wild (including collection vessels and transport facilities), facilities for captive breeding and culturing (including running seawater systems and water quality controls), and for outplanting or larval release (see Box 2.1). This infrastructure is largely available from ongoing restoration efforts but is limited to places with marine laboratories or private coral husbandry operations. Organizations such as SECORE are developing techniques for larval rearing in *in situ* pools and substrates to improve settlement (Margaret Miller presentation to committee). Well-equipped research facilities are also necessary to better understand managed breeding outcomes down through several generations.

GAMETE AND LARVAL CAPTURE AND SEEDING

What It Is

Gamete and larval capture and seeding is a specific way to enhance the natural sexual reproductive processes of corals by using natural spawning events to supply gametes for future use or larvae for settlement and laboratory growth. Corals reproduce primarily through sexual processes that result in coral planula larvae. Because corals are sessile, benthic organisms, the production of these motile propagules is essential for dispersal and population replenishment (Harrison, 2011). The vast majority of corals are broadcast spawners, releasing gametes (eggs and sperm) into the water column where fertilization and development occur (Harrison et al., 1984; Harrison, 2011; Richmond and Hunter, 1990). A few coral species brood their planula larvae following internal fertilization, and there is evidence that in some cases parthenogenesis may also occur. Larvae formed by spawned gametes take between 18 and 72 hours to fully develop to the ciliated planula stage, while brooded larvae are fully competent to settle and metamorphose upon release from the parent colony (Richmond et al., 2018). The timing of spawning events is highly predictable, allowing for the collection of gametes and larvae (dela Cruz and Harrison, 2017). Both larvae and gametes can be collected under laboratory conditions or *in situ*.

Benefit and Goals

Gamete and larval capture and seeding can be used to augment other interventions described in this report, but it also has its own advantages. Advances in coral propagation, including gamete and larval capture and rearing, support efforts for reef restoration (Barton et al., 2017; Chamberland et al., 2017). The benefits of gamete and larval collection include:

(1) Enhanced levels of fertilization of coral eggs compared to rates that would occur in nature, producing large quantities of larval seed material;
(2) Targeting of desirable genotypes or species for selective seeding efforts;
(3) Providing the material for controlled crosses of gametes to select for resistance attributes;
(4) Producing larvae for manipulations including chimeric coral colonies and hybrids (described in the Managed Breeding section on hybridization between species); and
(5) Obtaining "clean" larvae devoid of zooxanthellae in species that have horizontal transmission of algal symbionts, to allow for selective infection with specific types (described in the Algal Symbiont Manipulation section in Chapter 3).

In light of the downward trajectory in live coral cover of many reefs, gamete and larval capture efforts can be of particular value for reefs where populations have declined and the Allee effect—the decrease in gamete density and subsequent fertilization of eggs—occurs. This approach is appropriate for *Acropora* in the Caribbean and Atlantic, where natural recruitment levels have been extremely low and populations of adults are at low densities and patchy (Baums et al., 2005; Williams et al., 2008). These tools can support the goal to achieve population sizes that are eventually self-sustaining.

How to Do It

For laboratory-based efforts, coral adults can be collected from the field just prior to predicted spawning. For many corals, egg-sperm bundles are released, which float to the water's surface. They can be collected using containers with fine mesh (e.g., 10 μm), which traps eggs and allows sperm to pass through. By separating the sperm and eggs, their density can be controlled and selective seeding or crosses made (dela Cruz and Harrison, 2017; Pollock et al., 2017).

In the field, there are a number of ways of collecting gametes. Tents of fine mesh can be placed over gravid colonies, with a float and chamber at the top (Figure 2.3; Sharp et al., 2010). As egg-sperm bundles are released, they float and can be captured. These can then be crossed with gametes from another colony of the same species, which has been shown to yield higher fertilization rates than efforts at self-crossing in colonies that are simultaneous hermaphrodites (Heyward and Babcock, 1986).

Following development, fully competent coral larvae can be seeded directly onto reefs using mesh enclosures, they can be transferred to reefs on settlement plates from controlled recruitment efforts, or released onto appropriate substrata *en masse,* particularly in cavities, cracks, and crevices where the larvae are likely to be retained and recruited (dela Cruz and Harrison, 2017).

FIGURE 2.3 A mesh tent used for *in situ* collection of coral gametes during spawning events. SOURCE: Sharp et al., 2010.

Current Feasibility

The technologies and techniques for gamete collection and fertilization have already been developed, although they require improvement to achieve the appropriate scale to make this approach a viable intervention. Additional efforts and experiments on larval distribution and reef seeding are needed, as few successes have been reported to date. One recent experiment demonstrated that successful in-tank, closed-system spawning is possible with careful replication of seasonal temperature, lunar cycle, and photoperiod conditions, with a high degree of variability in success across species (Craggs et al., 2017). While some studies found low levels of success with seeding trials (Edwards et al., 2015), others suggest this remains a promising option for interventions (dela Cruz and Harrison, 2017). Recent advances in cryopreservation of gametes is a critical step forward in allowing for gene flow among distant populations (Hagedorn et al., 2017).

Potential Scale

Presently, the spatial scale for gamete collection is at the level of reefs over hundreds of meters, and for reseeding at tens of meters. This can represent millions of gametes and translate to thousands of recruits and considering mortality, tens to hundreds of mature coral colonies. For most reef-building corals used in such efforts, where the creation of habitat and rugosity are the key targets, spawning may occur only once per year for a single or a few days. Some of the planulating species have extended periods of larval production, from several months to year round. Acroporid corals are good species due to their branching and table morphologies, high growth rates, and wide distributions, but these often have very limited spawning periods.

Risks

There are few environmental risks when using locally sourced corals as studies have found most coral reefs are self-seeding. Although coral planulae may remain competent for weeks and even months, efforts to collect gametes and raise larvae for seeding the reef of origin can be considered simply facilitation and augmentation of natural processes. If gamete and larval capture and seeding is used to support other interventions, the risks of those interventions apply. The risks for selecting resistant genotypes or species for supportive breeding and hybridization are discussed in the Managed Breeding section in this chapter. Introducing larvae from distant reefs raises the same issues discussed in the Managed Relocation section (Chapter 4).

Limitations

Limitations are mostly related to infrastructure, labor costs, and species availability. Labor for collecting gametes and larvae is intensive and can be costly. The approach is also limited by the availability and identification of preferred phenotypes, genotypes, or species in an area. Finally, for species in which larvae and recruits acquire their algal symbionts from the environment (horizontal transmission), there is no guarantee the most suitable zooxanthellae will be available for laboratory-raised stock.

Infrastructure

There is a range of infrastructure needs, depending on the goals, objectives, and scales of interventions. Localized seeding projects can be undertaken with limited resources, including small boats, buckets, plankton nets, and inflatable pools. The more complex efforts of managed breeding and controlled zooxanthellae infections require well-equipped laboratories, flowing seawater systems, and supplies commonly associated with aquaculture facilities.

CORAL CRYOPRESERVATION

What It Is

Coral cryopreservation is the process by which gametes, embryos, or other living materials are frozen in such a way that they remain viable after being thawed. Much of the effort for corals has focused on gamete cryopreservation, particularly sperm (for which methods are better developed) (Hagedorn et al., 2017; Viyakarn et al., 2018). There have been some efforts to test methods to cryopreserve embryonic material (Hagedorn et al., 2006, 2012) and adult tissues (Feuillassier et al., 2014a, 2014b). Algal symbionts from three coral species have also been cryopreserved (Hagedorn et al., 2015).

Benefit and Goals

Living corals are continuing to decline, and as a result, there is a risk of losing the genetic variability at the population and species level that will be essential for restoration of coral reefs, both in the short term under compromised conditions and over the longer term when environmental conditions hopefully improve. Cryopreserved material can also be used to later increase genetic variation in critically endangered species, as was done, for example, with the recovery of black-footed ferrets (Howard et al., 2016). The rationale for long-term storage of frozen material as an insurance policy is the same as that which exists for other conservation-based cryopreservation efforts, such as seed banks (although it should be recognized that as conditions change the variants common today may not be fit in the future). However, cryopreserved material can also be used for assisted gene flow and for research purposes, and thus should not be viewed simply as a last-ditch effort to prevent extinction (Hagedorn et al., 2017). In addition, cryopreservation of gametes (e.g., sperm) allows for fertilization between species that in nature do not live close together or that spawn at different times.

How to Do It

The chief challenge with cryopreservation is avoiding damage to cells caused by ice formation during freezing. To avoid ice damage, cryoprotectants such as dimethyl sulfoxide and propylene glycol are introduced during the cooling process. Optimizing the process requires empirical testing of cooling rates (which may be relatively slow or ultrafast, resulting in vitrification), thawing rates, and types and concentrations of cryoprotectants (Hagedorn et al., 2012; Hagedorn and Carter, 2016; Viyakarn et al., 2018).

Current Feasibility

Several algal symbionts and sperm from at least 16 species of coral have been successfully cryopreserved (Hagedorn and Carter, 2016; Hagedorn et al., 2017), as have embryonic cells (Hagedorn et al., 2012). There have also been preliminary tests of methods for larvae (Hagedorn et al., 2006) and small pieces of adult corals (Feuillassier et al., 2014a, 2014b) but these have not yet achieved success. Creation of viable embryos through fertilization of eggs with cryopreserved sperm is feasible now (Hagedorn et al., 2017), but other approaches are still in the developmental stage.

Potential Scale

Cryopreservation is a delicate process and requires careful technique in order to ensure that material is viable once thawed. It is thus done at the scale of a single individual organism or pool of gametes (that is, it is not currently feasible to bulk preserve large amounts of adult coral).

However, once frozen, material can be 2 to essentially anywhere. Hagedorn et al. (2017) found that sperm frozen for up to two years was as viable as sperm frozen for less than 1 month, suggesting that when done well, cryopreserved material can be stored for years and remain viable, although very long-term tests of storage efficacy have not been done.

Risks

The material being frozen and subsequently thawed has not otherwise been manipulated. For this reason, the risks of cryopreservation per se are minimal, apart from the fact that reliance on cryopreserved material creates vulnerabilities if for some reason the thawed material is later found to be inviable. However, cryopreservation will by definition not include genetic combinations that develop over time in response to changing conditions. More seriously, transport of cryopreserved material for use in other locations could potentially carry the risk of transferring other organisms including potential pathogens.

Limitations

Currently, coral cryopreservation is done at small scales as laboratory experiments and is largely restricted to sperm. Even in these cases, only a tiny fraction of extant diversity has been cryopreserved (16 coral species from the Caribbean, Hawaii, and the Great Barrier Reef; Hagedorn et al., 2017). Also, in the case of sperm, cryopreservation currently decreases fertilization success by about 50%, so it is important to start with fresh, highly mobile sperm (Hagedorn et al., 2017). Finally, scientists doing cryopreservation work are often not in close contact with initiatives actively engaged in restoration (Hagedorn et al., 2017).

Infrastructure

The infrastructure needed is widely available as cryopreservation has been developed for other organisms, including plants, agricultural and aquacultural animals, and humans; primarily this involves specialized temperature-control equipment so that precise rates of freezing and thawing can be achieved. Storage facilities for frozen material are also needed; for large-scale efforts this involves frozen biorepositories such as the Taronga Zoo’s CryoDiversity Bank currently being used for coral.

GENETIC MANIPULATION

What It Is

A novel way forward to potentially “design” more resilient corals than currently exist in nature relies on the use of genetic manipulation methods. Genetic manipulation is the direct alteration of the genome of an individual organism, which might be the coral or its algal symbiont. Modern laboratory-based approaches to genetically modify an organism involve genome editing through zinc finger nucleases, transcription activator-like effector nucleases, and CRISPR/Cas9 gene editing (Gaj et al., 2013). Modern genetic manipulation systems contrast with classical genetics, which usually relies on identification of naturally occurring variants or the use of mutagens to generate novel phenotypes, which are identified by screening assays. Modern genetic tools can be used to insert gene drives, which use novel genetic constructs to create a biased system of inheritance by enhancing passage of a selected genotype to offspring (NASEM, 2016a). More broadly, genetic manipulation may be used as a tool to significantly expand knowledge about the genetic underpinnings of coral biology by allowing for detailed studies to understand the function of particular genes of interest.

The massive current interest in genetic manipulation is fueled by developments in CRISPR/Cas9-based genome-editing, and now transcriptome-editing (Konermann et al., 2018), that can be applied to a wide variety of organisms to generate loss-of-function mutations or to modify existing genes down to the single-nucleotide level (Doudna and Charpentier, 2014). CRISPR/Cas9 gene editing allows deletion, addition, or modification of existing genes and has been readily implemented in a wide variety of organisms such as yeast (DiCarlo et al., 2013), rockcress (Feng et al., 2013), and fruit fly (Gratz et al., 2013). The potential application of this RNA-programmed approach to genetic modification was described in a landmark article by Jinek et al. (2012).

Benefit and Goals

The goals of genetic manipulation are to alter specific genes in corals, their symbionts, or their associated microbiome in order to manufacture higher levels of stress resilience than can be found in nature. These goals depend on transformation technology to introduce genes and genetic constructs in corals or their symbionts, alteration of the coral or symbiont genomes in defined ways, and growth of genetically homogeneous colonies with the ability to pass these altered genes on to the next generation. If a genetically diverse population of a coral species is targeted with CRISPR/Cas9 methods, it may be possible to maintain the standing genetic variation at nontarget loci while propagating desirable traits into the environment. CRISPR/Cas9 substantially simplifies the process of genome editing because it relies on a very short RNA-coding region for target specificity (Doudna and Charpentier, 2014; Ran et al., 2013).

An additional goal is to use genetic manipulation to experimentally test hypotheses about the susceptibility of corals to stress and to identify the genetic causes of individual- or species-level variation in stress tolerance. This can also be applied to the algal symbiont, which plays a significant role in the bleaching response in corals. The major goal of symbiont genetic manipulation will be to uncover the rules underlying the algal symbiont response to reactive oxygen species or thermal stress (e.g., antioxidant genes such as iron-type superoxide dismutase) that can be manipulated (e.g., over-expressed) to reduce bleaching susceptibility in colonies. If genetically modified symbionts can be generated that are hardened to environmental stress, they could be introduced into coral animals to protect them in the natural environment.

How to Do It

CRISPR/Cas9 is the only tool to date that has been used to directly alter a coral genome. The essential components of the CRISPR gene-editing system are a short noncoding guide RNA (gRNA) and the Cas9 protein. The gRNA is designed to be homologous to the specific genomic location of interest. This homology guides the gRNA/Cas9 protein complex to that genomic location where the Cas9 protein induces a break in the DNA, where insertions or deletions can be made as the break is repaired by the cell's repair machinery (Li et al., 2013). Homologous sequences present either elsewhere in the genome, on extra-chromosomal elements, or on foreign oligonucleotides can invade the Cas9-cut DNA and allow the incorporation of foreign sequences at the target site (Li et al., 2013).

CRISPR/Cas9 in Corals

A single paper on CRISPR/Cas9-based genetic manipulation in corals has until now been published (Cleves et al., 2018) and it provided preliminary proof-of-concept data using the model species, *Acropora millepora*. These authors targeted the genes encoding fibroblast growth factor 1a, green fluorescent protein, and red fluorescent protein. Fertilized eggs of *A. millepora* were injected with appropriate single guide (sg)RNA/Cas9 complexes. The results showed partial deletion mutation induction in 50% of larvae. All of the successfully altered larvae had deletion mutations that were heterozygous genetic mixtures of the wild type and several kinds of altered genes. Although the prospect of raising homozygous mutants through genetic crosses is challenging, the introduction into wild populations of beneficial alleles in heterozygous individuals may be sufficient to increase coral resilience. The generation of homozygotes would of course be very important to understand gene function but may not be necessary to improve coral health. Given these uncertainties, it is currently unclear how genome editing will impact coral research and restoration. Nonetheless, a lot was learned through this pioneering study that could contribute to a long-term goal to generate genetically modified lines that are stable, adapted, and environmentally resilient.

CRISPR/Cas9 in Dinoflagellate Symbionts

Transformation protocols (e.g., for transgene expression) and CRISPR/Cas9-based genetic methods are also being developed for the dinoflagellate symbiont of corals (Levin et al., 2017), but no publications have yet resulted from the work. Potential targets for modification include genes that respond to thermal stress such as superoxide dismutase, ascorbate peroxidase, and other antioxidants (Wietheger et al., 2018).

CRISPR/Cas9 in Bacterial Components of the Coral Holobiont

Genetic engineering of the coral microbiome using CRISPR/Cas9 methods is another potentially powerful approach to improving coral resilience. However, CRISPR-induced double-strand breaks (i.e., both strands of the DNA duplex are broken) are lethal in bacteria because of the low efficiency of the repair pathway (known as non-homologous end joining) in these taxa. This has led researchers to engineer bacteriophage-derived recombination proteins in model species such as *Escherichia coli* to provide the needed function. These recombination-mediated genetic engineering (recombineering) methods are rapidly developing (Li et al., 2016). There is potential, therefore, to engineer traits into bacteria that can be beneficial for coral fitness (i.e., enhanced antioxidant activity), and then inoculate these bacteria into the coral microbiome. However, such approaches have not yet been tested, and require a far greater understanding of the coral microbiome and the ability to specifically manipulate the microbiome and maintain these shifts and conferred benefits (see the Microbiome Manipulation section in Chapter 3).

Current Feasibility

The basic mechanism of genetic manipulation with CRISPR/Cas9 has been demonstrated in corals (Cleves et al., 2018) and is well known as a tool in basic developmental biology of other cnidarians (Ikmi et al., 2014). To date, success using CRISPR/Cas9 in corals has been limited to mosaic creation of deleted gene segments in early larvae. No demonstration of altered phenotypes from manipulation and no demonstration of incorporation of manipulated genes into an adult coral have yet been published. A key area of future focus should be shortening the generation time in corals, perhaps using mutagenesis or identifying culture modifications that enhance the rate of development, as has been done in *Arabidopsis* (Ochatt and Sangwan, 2008).

Feasibility for enhancing coral resilience will be dependent on the identification of clear gene targets hypothesized to be able to alter coral resilience through changes to a single gene or multiple genes in the same or different pathways. There are a wide variety of gene expression changes that have been documented during acclimation and adaptation to high-temperature conditions (Barshis et al., 2013), and a large number of changes in transcription factors likely to have multiple downstream effects soon after heat exposure (Traylor-Knowles et al., 2017). Pivotal pathways that might be important in switching from heat resistance to bleaching include the genes for heat shock proteins controlled by the heat shock factor (Louis et al., 2017), genes that control the unfolded protein response (Ruiz-Jones and Palumbi, 2017), genes associated with reactive oxygen species (ROS) production (Oakley and Davy, 2018), and others. However, differences between populations in resilience-related genes suggest that heat resistance is a multilocus phenotype controlled by tens or hundreds of genes (Bay and Palumbi, 2015; Dixon et al., 2015), so simple target genes with large temperature effects are not documented to date. One exception is a single allele discovered by Jin et al. (2016) to have a strong association with the oxidative state, potentially mediating ROS damage during symbiotic breakdown. CRISPR/Cas9 could be used as a technique to test this hypothesis as a starting point in further development. A potential avenue for identifying target genes for genetic manipulation is through the use of gene co-expression networks (an analysis to identify genes with similar expression pattern). These methods can help identify "hubs" of gene expression that impact downstream traits such as the cell cycle and stress response (Stuart et al., 2003; van Dam et al., 2018). These hub genes offer opportunities, for example through over-expression, to potentially enhance complex phenotypes such as the coral thermal stress response.

Manipulations of coral dinoflagellate symbionts appear to be less feasible. ten Louhis and Miller (1998) reported genetic transformation of *Symbiodinium* cells, but later attempts have not successfully repeated this result (Levin et al., 2017). A variety of problems have been proposed to explain the large hurdle of *Symbiodinium* transformation, including the thick cell wall, the atypical chromosomal structure, and the large evolutionary divergence of *Symbiodinium* to other tractable algal systems. In addition, as in corals, the best genes to target for *Symbiodinium* manipulation have not yet been identified.

Potential Scale

Initial trials of genetically modified corals or symbionts would occur at the individual colony or culture level. Once a modification was successfully accomplished, it would be individually tested for improvements in resilience. Thereafter, the modification is expected to be propagated through clonal growth or sexual reproduction into a population of corals that would be planted into a nursery population. Once the propagated genetic modification was tested for high stress tolerance, larger groups could be generated. Each phase of this amplification is likely to take 3-7 years, in particular if growth of corals to sexual reproduction is involved. Asexual propagation (e.g., repeated fragmentation) of genetically modified resilient corals might decrease the amount of time.

These changes would apply to a single modified gene. If modification of more than one gene was deemed necessary—and tests of heat tolerance suggest multiple loci are involved—then multiple modifications might need to be done in series. Alternatively, if done in separate lines, these distinct modifications would need to be combined in a single zygote through rounds of sexual reproduction. Because serial modification, or combination of separate lines through gamete fusion, would require sexual reproduction, each stage would take 3-7 years (e.g., Kojis and Quinn, 1981). This timeframe would slow deployment of multigene adaptive manipulations and reduce the number of modifications that could be rapidly deployed. These steps would apply to a single species, and would need to be completed separately, perhaps with separate genetic target loci, in different species.

Modifications to symbionts may be easier to scale up. If a symbiont with broad ability to colonize many coral species were to be conferred with a gene for heat tolerance, it might be able to be added to the holobiome of many different adult coral colonies or multiple species quickly if the original heat-sensitive symbiont could be replaced, because 85% of corals recruit the symbiont algae each generation.

Risk

The application of gene drives in field conditions is still controversial. This is due to ethical considerations and potential negative ecosystem impacts resulting from the release of genetically modified organisms that may spread undesirable traits among natural populations (e.g., NASEM, 2016a; Pugh, 2016). Unintended consequences are virtually impossible to predict *a priori*. For example, the gene drive could inadvertently impact other characteristics, such as the ability to transmit or withstand pathogens or other stressors (Kuzma and Rawls, 2016). Another potential risk is drive resistance that can result from mutations that block cutting by the CRISPR nuclease (Noble et al., 2018). Resistance can arise from standing genetic variation at the drive locus or because the drive mechanism is not perfectly efficient and is predicted to prevent drive fixation in wild populations. The accidental release of gene-drive organisms by scientists poses unknown risks at this time (Callaway, 2017; Esvelt and Gemmell, 2017; NASEM, 2016a). Finally, an unintended risk of gene drives is the slow pace of development with coral models. Given that field deployment of modified individuals may take up to a decade, this method will not address immediate risks to corals and therefore be less effective in the short-term.

Polizzi et al. (2018) identified 13 potential risk factors associated with gene drives. Several of these may be relevant in the coral context, as noted below:

- Unexpected gene transfer: Efforts would be made to prevent the unwanted transfer of genes to other species, but it cannot be ruled out.
- Evolution: Resistance may be conferred in the short term and organisms may behave as expected, but it is impossible to plan and mitigate for the unexpected.
- "We don't fully understand": Although the technology is rapidly advancing, there are still many known unknowns (e.g., extent of off-target [nonspecific] genome editing), and an unknown number of unknown unknowns.
- Ecosystem effects are challenging to predict: Changing a coral community has many uncertainties and predicting how those changes will interact with wider ecosystems is virtually impossible.

Limitations

The discussion of methods, feasibility, and scale listed above reveal a host of limitations of the current technology of gene manipulation. Summarizing from the above:

(1) Current CRISPR/ Cas9 technology has been demonstrated in corals but not symbionts. In addition, generation of homogeneously modified corals, and the delivery of these genes to offspring has not yet been successfully accomplished.
(2) Gene targets for coral or symbiont manipulation are not clear. However, gene expression followed by gene manipulation methods are powerful ways of testing which genes are the best to manipulate. Such hypothesis testing will be crucial but time consuming.
(3) The small number of stress-resistance genes with large phenotypic effects reduces the likelihood that a single gene manipulation will provide substantial stress tolerance. Instead, current knowledge of the genetic architecture of coral stress genes suggests that multiple gene manipulations may be necessary. Such multiple manipulations are within the ability of current gene technology and animal husbandry protocols, but are time consuming.

These limitations are similar to those facing plans to genetically modify other animals introduced into the wild (salmon, mosquitoes, etc.), but are in some cases more severe because of the need to manage multiple genes and multiple species.

This approach is limited in its ability to develop resilience in corals in the near-term due to the timeframe of research and development needed. An incremental approach where one species (i.e., a well-characterized "model" coral) is used to manipulate a small number of genes may be an appropriate initial plan. This initial plan would not save a substantial number of reefs by itself, but over a period of 10 years might lay the groundwork for other genes and species to be more quickly modified.

Infrastructure

Research infrastructure: Marine laboratories with access to test corals, husbandry facilities, long-term growout laboratories that can be used to generate sexually mature colonies, good molecular biology laboratories, microscopy, symbiont culture facilities, and other facilities would need to be available for each species and each ocean region.

BioInformatics infrastructure: Genetic manipulation requires a well-known genome sequence for each species used, the ability to probe genome changes, and the ability to follow phenotypic, genotypic, epigenetic, and genetic changes across multiple generations.

Collaborative infrastructure: It may be that a single laboratory at a single location will be able to achieve the initial success at manipulating one coral species at one gene, with resulting heritability and phenotypic change. However, it is most likely that it will take a consortium of laboratories across many countries to achieve, multispecies, multigene success. This collaborative effort would require parallel facilities and parallel approaches in different nations, and would take advantage of the different coral spawning opportunities in different parts of the world and different husbandry facilities. Different laboratories may need to test different genes for their ability to confer increased stress tolerance, with the idea that negative results would be considered a strong benefit to the consortium as a whole. A successful example of such an initiative is The Arabidopsis Information Resource (https://www.arabidopsis.org) where a wide variety of genetic and genomic resources are stored and shared for a model plant species. A parallel, coordinated effort can lead to the creation of a model coral to establish fundamental knowledge about its biology and genetics that can be used to widen analyses to a plethora of other important species. The value of having a well-annotated, manually-curated, and high-quality genomic and genetic resource for a coral species cannot be overstated in terms of supporting all downstream genetic and ecological manipulations.

3

Physiological Interventions

The coral holobiont is the result of a complex metagenome comprising the coral host and its algal symbionts and the other microbiome members including fungi, prokaryotes (bacteria and archaea), and viral components. Reef corals respond to changes in their environment through mechanisms that can originate either in the coral host or in its microbiome. Consequently, reef coral health and function depend on the responses of, and interactions between, all of these partners. Here we describe potential interventions that can influence the physiological responses of reef corals without changing their individual genomes. This includes pre-exposure of the holobiont to environmental stress to elicit compensatory responses that increase their resistance or resilience to future stress, changes in the composition of reef coral metacommunities (in favor of more stress-tolerant algae, or other microbes with therapeutic benefits), and the use of antibiotics, phage therapy, antioxidants, and nutritional supplements.

These novel approaches can compensate for the impacts of environmental stress in different ways and at different points in the stress response. For example, oxidative stress caused by high temperatures might be avoided by hosting more thermotolerant algal symbionts or having higher constitutive expression of heat shock proteins. Alternatively, high levels of oxidative stress might instead be managed using beneficial bacteria to detoxify reactive oxygen species as they are produced. Finally, bleached corals might be treated with nutritional supplements to help them recover from bleaching. These different interventions vary in their longevity, with the effects of some triage-based activities being short-lived (days to weeks), while other activities might be longer-lasting (months to years). Some interventions might have effects that remain for the lifespan of the coral host (typically decades), while others might have impacts that are passed on to future generations.

PRE-EXPOSURE

What It Is

Various terms have been used to describe the processes by which prior exposure of an organism to certain (usually stressful) environmental conditions induces a response that better prepares it for subsequent re-exposure. These terms include “pre-exposure,” “pre-conditioning” (or sometimes just “conditioning”), “induced acclimatization,” “priming,” “stress hardening,” and even just “acclimation.” Additional terms have also been used to refer to the mechanisms by which these responses are achieved (e.g., “constitutive upregulation” or “frontloading” for gene expression) or to refer to the observable change in organisms that results (e.g., “phenotypic plasticity” for physiological or morphological responses). Here, we use the term “pre-exposure” as a general term to refer to the deliberate exposure of an organism (in this case, reef corals and their symbionts) to conditions that might, by whatever mechanism, confer some degree of additional tolerance to subsequent re-exposure of the organism (or in some cases, its progeny) to the same or similar conditions. This term places the emphasis on the initial exposure itself as the intervention being considered, rather than the mechanism by which the increase in tolerance is achieved (whether it be genetic, epigenetic, physiological, behavioral, etc.). The initial exposure can be either acute or chronic, might involve multiple stressors, and could involve either a single shock exposure or incremental increases over time. The induced response prepares the organism for conditions that may also be either acute or chronic. Given this wide variety of exposure-response combinations, it is to be expected that different mechanisms will vary in their importance depending on the timescales involved in both exposure and response.

Benefit and Goals

It has long been recognized that prior exposure of organisms to stressful conditions can shape their response to subsequent re-exposure to the same or similar conditions. In fact, this phenomenon is so fundamental that its existence can be argued from first principles: if organismal responses to stress are designed to help them compensate, then the degree to which these responses prepare the organism for subsequent exposure to the same stress is simply dependent on how long the organism maintains the response once the initial exposure has ended.

In reef corals, evidence demonstrating that pre-exposure has a beneficial effect (whether or not the specific mechanism is known) is widespread. It is well known that corals in lagoons and on reef flats routinely experience high temperature and high light stress (and sometimes high or low salinities and aerial exposure), resulting in individuals that are tolerant of thermal bleaching events, although the relative contributions of local selection versus pre-exposure can be difficult to determine (Palumbi et al., 2014). That some part of this response is due to pre-exposure was first shown by Brown et al. (2000), who found that reef flat coral surfaces chronically pre-exposed to high solar irradiance by virtue of facing west versus east were more resistant to thermal bleaching, indicating that prior experience of chronic stress could shape the response of corals to acute stress of a different (but related) variety, even when they were the same genotype (see also Brown et al., 2002).

Over larger scales, coral reefs prone to high temperature variability tend to experience less bleaching in response to episodic thermal stress than reefs with more constant temperatures (McClanahan and Maina, 2003; McClanahan et al., 2005, 2007; Safaie et al., 2018). This indicates that certain pre-exposure regimes, such as high temperature variability, can be beneficial in producing corals that are better able to deal with acute stress, although the longevity of the protective effect and the role of selection versus acclimatization remain difficult to determine. Similar conclusions are also implicated in the discovery by Ainsworth et al. (2016) that temperature regimes that pre-expose reefs to mild thermal stress (above the maximum monthly mean temperature, but below the bleaching threshold) for short periods (1-2 weeks) can protect corals from subsequent bleaching a few weeks later, provided the initial pre-exposure is followed by a brief “recovery” period of cooler temperatures. Pre-exposure of corals to high irradiance may also help protect them from bleaching through the production of photoprotective fluorescent proteins, which can reduce oxidative stress on corals (Salih et al., 2000, 2006).

The value of pre-exposure as an intervention strategy to increase the resilience of coral reefs (largely by pre-exposure of corals to high temperature or high light to increase their bleaching tolerance) remains dependent on how long the compensatory response lasts once the initial exposure has ended (or how readily chronic exposure can be maintained). This, in turn, is likely to be dependent on the mechanisms involved. Four types of mechanisms can be broadly distinguished: (1) acclimatory changes in gene expression, (2) adaptive changes in gene expression, (3) epigenetic modification, and (4) changes in holobiont composition. These phenomena are described in Box 3.1 and in the Algal Symbiont Manipulation section. Although some of these mechanisms, such as acclimatory changes in gene expression, can result in compensatory changes that can be almost instantaneous and highly reversible (e.g., the upregulation of genes expressed in basic metabolism or cellular function in response to higher temperature), other changes can take much longer to develop and can potentially last much longer. These include changes in gene expression that result in structural changes to gross morphology or cellular architecture (especially in early ontogeny) and adaptive changes in gene expression that can be permanent due to DNA alterations (eQTLs). Other long-lived changes include epigenetic modifications (that can sometimes be heritable), and changes in symbiont diversity or dominance. All of these changes can apply to different members of the coral microbiome, not just the coral host itself. For example, physiological changes in algal symbionts exposed to high light include changes in the abundance of symbionts, the amount of chlorophyll per cell, the size of photosynthetic units, and xanthophyll cycling capacity (Brown et al., 2002), all of which can influence the subsequent bleaching tolerance of the coral host, while also differing in how long these responses last.

BOX 3.1
Mechanisms of Stress Response

The role of differential gene expression

Gene expression analysis provides a straightforward and inexpensive method to assay the response of corals to environmental change or to understand the genetic controls of development and biomineralization (e.g., Mass et al., 2016). Current approaches usually rely on sequencing millions of cDNA fragments using the Illumina platform; this is referred to as RNA-Seq. Gene expression alterations can be divided into three broad categories: (1) Short-term responses act in the timeframe of minutes to hours and are readily reversible. These have been the target of most transcriptomic studies to understand basic metabolic processes and reconstruct these pathways (described further in the next paragraph). (2) Acclimatory gene expression is the result of long-term pre-exposure that can be maintained for weeks or months post-exposure under selection for that trait. These traits (e.g., resistance to thermal stress) are often explained by epigenetic modification and may not be trans-generational, being reversible once the specific selective constraint is removed or the environment changes. (3) Adaptive gene expression is the result of permanent changes to gene expression due to changes in the frequencies of gene regulatory variants or other DNA-based controls of gene expression. These modifications are known as cis-regulatory expression quantitative trait loci (cis-eQTLs) and play a role in coral adaptation (Rose et al., 2018).

A typical short-term gene expression analysis was recently done by Hou et al. (2018) on *Galaxea fascicularis*. These authors raised corals 25°C (control) and 32°C (high temperature) and collected RNA-Seq data at 10 and 18 hours post heat-stress, as well as at 0 hours control.

Algal symbionts were rapidly expelled in response to heat stress. Over-represented gene ontology terms (i.e., classes of gene functions) under the treatment were related to the Unfolded Protein Response, likely due to free radicals produced by the symbiont, that could potentially lead to apoptosis and cell death. Some down-regulated genes were involved in the immune response, perhaps exposing the coral to pathogenic bacteria. Another study of coral gene expression was done by Mohamed et al. (2016) in which they studied genes related to symbiosome (the compartment that houses the algal symbiont) formation in *Acropora digitifera*. They found that when coral planulae were exposed to a competent Symbiodiniaceae, only 1,073 transcripts (i.e., less than 3% of the total transcriptome) were differentially expressed 4 hours after exposure and returned to baseline levels within 48 hours. Based on these RNA-Seq results it was proposed that the symbiosome acts as an arrested phagosome that protects the algal symbiont from host lysosomes.

Epigenetic modification

The field of epigenetics addresses modifications of nucleic acids that are not sequence-based yet confer adaptive advantages and may be transgenerationally inherited (Feil and Fraga, 2012). Epigenetics affords a strategy to generate multiple phenotypes from a single genotype, which may be prompted by pre-exposure. The mechanism that has been most often studied is DNA methylation, the addition of a methyl group (-CH_3) to DNA nucleotides—most commonly on cytosine in the sequence, CpG. The role of DNA methylation in stress-response regulation is supported by limited data from computer-simulated studies of *Acropora* (Dixon et al., 2014) as well as *Porites*, *Pocillopora*, and *Stylophora* (Dimond and Roberts, 2016), showing that strong gene body methylation (GBM) is associated with housekeeping functions, whereas weak methylation is associated with response to environmental changes. The environmentally resistant *Montipora capitata* had stable growth and unchanged DNA methylation under low-pH conditions, relative to the more environmentally sensitive and physiologically plastic *Pocillopora damicornis*, indicating a role for DNA methylation in coral environmental sensitivity and phenotypic plasticity (Putnam et al., 2016). Dixon et al. (2018) used coral fragmentation and transplantation of 30 colonies between a warmer (near Orpheus Island) and a cooler (near Keppel Island) site on the Great Barrier Reef, Australia, to study the impact of environment on GBM and gene expression. Their results showed that the different genotypes of adult, genetically identical replicate corals impact both CpG methylation and gene expression patterns in *A. millepora*. They found, as others have done previously, that GBM correlates significantly with stable, active transcription with the minor proportion that shows variation potentially being linked to adaptation.

However, animals generally do not show strong patterns of CpG methylation linked to transgenerational inheritance, making it less clear how important this mechanism will be in corals (Torda et al., 2017). The most comprehensive study of transgenerational CpG methylation was done by Liew et al. (2018a), who traced the patterns of DNA modification in adult, eggs, sperm, and larvae from two populations of the brain coral *Platygyra daedalea* from a high-stress (Abu Dhabi) and a moderate (Fujairah) environment in the Arabian Peninsula. The broad outcomes of this study are as follows: (1) short-term (days), trans-generational CpG methylation changes occur in *P. daedalea* and, therefore, likely in all corals; (2) different sampling sites show different patterns of methylation, suggesting this mechanism is responsive to local selective pressure; and (3) the absence of a sequestered germline in corals opens up the possibility that somatic methylation pattern may play a large role in coral epigenetics and adaptation. This means that coral colonies may represent genetically differentiated individuals that harbor independently derived somatic mutations, as well as different patterns of methylation. The latter may confer different adaptive responses within a colony and would need to be studied across individual polyps.

It appears that GBM plays a role in coral adaptation and transgenerational inheritance but it is a small effect and of unclear importance given the absence of a sequestered germline in a coral colony. GBM is a stable feature of coral gene regulation that marks highly expressed genes across generations. In terms of conservation, these results suggest that mass culture of corals under stressful conditions may allow the exploitation of GBM variation to identify the most resistant genotypes.

eQTLs and adaptive gene expression

Gene expression in corals is notoriously controlled by local environment (DeSalvo et al., 2008; Meyer et al., 2011), time of day (Brady et al., 2011), symbionts (Yuyama et al., 2012) and other factors. However, some potentially adaptive differences in gene expression between heat-tolerant and heat-sensitive corals are not environmentally induced, but are determined by the genetic makeup of the coral itself. For these genes, coral transplants retain their native gene expression patterns even in a new environment. One way for gene expression patterns to be fixed within individuals but variable between individuals is for expression of a gene to depend on the alleles for that gene that an individual possesses. These are often called eQTLs (Fraser, 2011). In corals, gene expression levels associated with bleaching resistance can be controlled by the alleles a coral has for that gene, providing a mechanism for the inheritance of adaptive gene expression differences (Rose et al., 2018). Often genes display both allele-specific expression and environmentally controlled expression (Palumbi et al., 2014), and the degree of genetically determined versus environmentally variable expression ranges widely across genes involved in bleaching. For genes with expression tied solely to heritable alleles (even those that are epigenetically altered by, say, methylation patterns), both natural and artificial selection can easily occur. For genes with expression tied to the local environment, conditioning of corals by placing them at high temperature can effect beneficial gene expression changes, but these may be temporary.

How to Do It

Pre-exposure interventions can be divided into three general categories that vary in their approach and differ in the degree to which they can be effectively implemented or scaled. The first approach (and most ambitious from the point of view of scalability) is acute pre-exposure. This involves the short-term exposure (typically days to weeks) of corals (at the larvae, recruit, or adult colony stage) to certain conditions at a specific time in order to trigger a response with long-lasting effects. The timing of the exposure may be key. Examples include exposing adult corals to high temperatures during gametogenesis or larval development, rearing larvae or settling recruits under stressful conditions prior to their release to the reef, or bleaching corals during early spring and allowing them to recover on the reef during the warming summer months. The second approach is chronic pre-exposure, which involves the long-term (months to years) exposure of (typically adult) corals to a particular set of conditions with the expectation that corals will trigger a variety of mechanisms which might together result in tougher corals. An example is the establishment of coral nurseries in relatively stressful (e.g., inshore) environments designed to effectively anticipate future conditions experienced by corals once outplanted.

The third approach is to assume that natural environmental variation already experienced by corals in the wild results in individuals that have already benefited from pre-exposure, and to exploit the benefits of this long-term (years) pre-exposure when identifying corals for restoration. An example is sourcing corals from local environments that have already been exposed to stressful conditions and prioritizing these for grow-out in a nursery. This latter approach shares some aspects with managed selection, but focuses on the benefits of site-specific acclimatization, although the difference may be hard to recognize without genetic testing.

Current Feasibility

Pre-exposure is currently feasible in the laboratory or in small-scale restoration efforts. Acute exposure in the laboratory is technically feasible at small scales, requiring informed decisions regarding life stage, duration, and degree of stress. Establishing coral nurseries in naturally stressed environments is more easily implemented because it is essentially a matter of identifying an appropriate nursery location. Identifying corals that have been naturally “pre-exposed” to stress is less straightforward to implement because it requires some knowledge of coral distribution and environmental variation, but it is nevertheless still very feasible. Studies described in Box 3.1 show that coral react to stress on a cellular level, with varying degrees of longevity of the response.

Potential Scale

The different pre-exposure approaches vary in their scalability. This reflects the fact that, although the science behind these responses is well understood in most cases, no prescriptive strategies for pre-exposure have been developed or implemented. Methods of acute pre-exposure, such as stress-hardening corals in nurseries prior to outplanting, may be straightforward to test and implement on an individual basis, but hard to scale. This may be especially true for adult colonies because each individual must be managed and monitored to ensure appropriate dose. Pre-exposure in batches as part of a restoration outplanting program will help these activities to be scaled up, but it will still require significant expenditure of time and resources. Acute pre-exposure of gravid corals to particular conditions (in the expectation that their gametes or larvae will be more tolerant of these conditions) may be more scalable because pre-exposure of one colony may translate to hundreds or thousands of pre-exposed gametes or larvae. Similarly, pre-exposing larvae or recruits may be scalable, but only if an active larval rearing and seeding program is already in place.

Chronic pre-exposure of adult corals in the nursery phase as part of an outplanting program may be more readily scalable, because it only involves identifying an appropriate location for the nursery. Similarly, provenancing strategies that exploit existing environmental conditions to naturally pre-expose colonies to appropriate conditions may also be very scalable, and are similar to managed relocations, which are considered in Chapter 4. The pre-exposure value of managed relocations would be in addition to the value of any fixed (genetic) effect due to local selection at the source site.

Beyond the spatial constraints of scaling, the value of pre-exposure is likely to be limited by the effectiveness and longevity of the compensatory response. Certain types of responses (such as acclimatory and reversible changes in gene expression) might only last minutes to hours, while other types of responses (such as changes in symbionts and epigenetic modifications) might potentially last for the rest of the organism's lifespan, or even be passed on to the next generation (see Figure 3.1). Consequently, it is difficult to generalize.

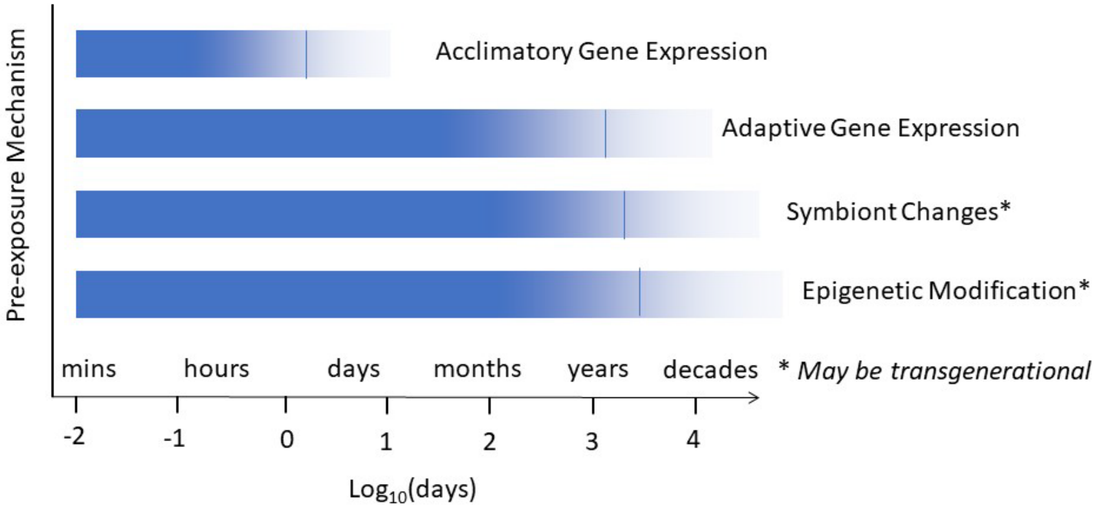

FIGURE 3.1 Conceptual representation of variation in the typical longevity of different response mechanisms induced following pre-exposure to stressful conditions. Typical longevity is represented by the vertical blue line within each horizontal bar. Variability in longevity is shown by the fade from left to right. Longevity (time) on the x-axis is represented using a logarithmic scale.

Risks

The principal risk of pre-exposure is that prior exposure to stressful conditions actually weakens the organism concerned, rather than strengthening it. This might result due to the expenditure of energetic resources used in activating the desired response and might be exacerbated by "overdoing" it—applying excessive amounts of stress in the pursuit of the beneficial response. The degree to which these risks are likely depends on the approach used and its anticipated mechanism. For some approaches, the likelihood of hormesis—where a beneficial response is induced following the application of a low dose of a stressor that would be harmful at higher doses—may be more likely than others. However, the majority of these approaches have not been attempted in the field and consequently the risk of "doing more harm than good" still needs to be tested.

Limitations

Pre-exposure approaches are largely limited by the ability to scale up in space and time. In almost all cases, longevity is likely to be influenced by the environmental conditions that the organism experiences following the initial period of pre-exposure. Conditions that are similar to those to which the organism was pre-exposed are more likely to extend the duration over which the compensatory mechanism remains in operation.

Infrastructure

Infrastructure needs depend on the life stage at which these pre-exposures might be implemented. Acute pre-exposure at the larval or recruit stage requires an active gamete/larvae collection and rearing program and an effective recruit seeding program. In contrast, chronic pre-exposure or managed relocation of adult colonies would require an effective nursery propagation and outplanting program.

ALGAL SYMBIONT MANIPULATION

What It Is

The algal symbionts of scleractinian corals (hard corals) have long been known to be diverse (Baker, 2003; Blank and Trench, 1985; Rowan and Powers, 1991). A recent revision of these symbionts recognized a new dinoflagellate family, the Symbiodiniaceae (LaJeunesse et al., 2018), comprising numerous genera corresponding to what were formerly clades of the single genus *Symbiodinium* (a genus that is retained to refer to certain members of clade A). To date, members of many of these genera (corresponding to former *Symbiodium* clades A, B, C, D, F, G, and H) have been detected in scleractinian corals (Quigley et al., 2018a), with multiple symbiont types occurring among different colonies of the same coral species (Rowan and Knowlton, 1995) and within colonies (Rowan et al., 1997). Different symbiont types have been shown to influence the stress phenotype of the host, particularly in response to high temperature (Baker et al., 2004; Glynn et al., 2001) or high light (Rowan et al., 1997) disturbance, and these are often reflected in the distribution of these symbionts over environmental gradients (Baker et al., 2004; Fabricius et al., 2004; Iglesias-Prieto et al., 2004; Rowan and Knowlton, 1995). These differences are most striking when the symbionts belong to different genera within the Symbiodiniaceae. However, differences in stress phenotype, both within genera (e.g., *Cladocopium*, formerly *Symbiodinium* clade C) and within species (Parkinson and Baums, 2014), also exist, indicating that functional diversity exists at many taxonomic levels (Suggett et al., 2017). It is now clear that corals of the same species hosting different symbionts typically vary in their physiological capabilities, and corals with stress-tolerant symbionts typically have higher bleaching thresholds. Thus, there have been attempts to manipulate algal symbiont associations to favor partnerships that confer stress tolerance to coral. The degree to which corals can change their symbiont communities in favor of these stress-tolerant partnerships, the coral life stage at which it is most appropriate to attempt these changes, and the consequences of doing so remain topics of active research.

Another approach that has been used to modify algal symbiont communities is to use artificial selection in the laboratory to experimentally produce symbiont lineages that are more thermotolerant (Chakravarti et al., 2017; Chakravarti and van Oppen, 2018). These symbionts can then be used for experimental manipulations involving corals, principally at the recruit stage, but also potentially in adults. Although conceptually similar in practice to many of the procedures outlined below, some of the risks associated with the use of this form of "experimental evolution" are more similar to those outlined in Assisted Gene Flow and Assisted Migration in Chapter 4, including certain genetic risks and tradeoffs, such as selection for one trait (e.g., high thermotolerance) coming at the expense of other traits.

Benefit and Goals

Changes in symbiont communities, at the individual colony level, can result in changes to holobiont phenotype, potentially helping corals respond to changes in the environment, such as higher irradiance (Baker, 2001; Rowan et al., 1997) or warmer temperatures (Baker et al., 2004; Berkelmans and van Oppen 2006; LaJeunesse et al., 2009). For example, bleached corals have been observed to recover with symbiont communities dominated by *Durusdinium* (formerly *Symbiodinium* clade D; LaJeunesse et al., 2018). This genus contains several thermotolerant species (e.g., *D. trenchii*, *D. glynnii*) that confer higher bleaching resistance to their coral hosts (Berkelmans and van Oppen, 2006; Cunning et al., 2015a, 2018; Glynn et al., 2001; Grottoli et al., 2014; Jones et al., 2008; LaJeunesse et al., 2009; McGinley et al., 2012; Rowan, 2004; Silverstein et al., 2015, 2017). Indeed, shuffling to *Durusdinium* can increase bleaching thresholds by approximately 1-2°C (Berkelmans and van Oppen, 2006; Silverstein et al., 2015). Corals with *D. trenchii* also appear to retain their symbionts during periods of cold stress, even though the symbionts are impaired, suggesting that some *Durusdinium* may also be resistant to expulsion in general (Silverstein et al., 2017). High- and low-temperature stress tolerance may be of benefit to corals in particular areas, for example Florida, where corals have suffered recent mortality as a result of both high- and low-temperature stress (Lirman et al., 2011).

How to Do It

Adult corals: Although changes in algal symbiont communities have been observed in the field, typically in response to coral bleaching (Baker et al., 2004; LaJeunesse et al., 2009) or transplantation (Baker, 2001; Berkelmans and van Oppen, 2006; Rowan et al., 1997), deliberate manipulation of symbionts in adult corals has to date only been achieved by duplicating these disturbances in the laboratory through controlled bleaching and recovery. These manipulations have exploited the fact that, while coral bleaching often leads to mortality when environmental stress (e.g., high temperature) is prolonged and/or severe, corals can recover their symbionts within a period of weeks to months if the stress is alleviated (Glynn, 1993). Moreover, the loss and subsequent re-establishment of Symbiodiniaceae communities through bleaching and recovery can present an opportunity for these communities to change (Baker, 2001; Buddemeier and Fautin, 1993), either through changes in the relative abundance of different symbiont types, or acquisition of different symbionts from the environment (symbiont "shuffling" versus "switching"; Baker, 2003). To date, three species of Caribbean coral (*Montastraea cavernosa*, *Siderastrea siderea*, and *Orbicella faveolata*) have been manipulated in the laboratory, by exposure to moderate heat stress (32ºC for 10 days), followed by recovery under cooler conditions. This "stress-hardening" treatment is a form of pre-exposure and is therefore conceptually similar to the pre-exposure interventions discussed earlier. Controlled bleaching and recovery boosted the abundance of *D. trenchii* from near 0% to over 99%, while causing almost no mortality in experimental corals (Figure 3.2; Cunning et al., 2015a, 2018; Silverstein et al., 2015). Moreover, the degree of symbiont community change could be reliably predicted based on bleaching severity and the photochemical advantage of one symbiont over another in the coral species in question. Methods for applying this approach to nursery-reared corals prior to outplanting as part of a restoration program are currently undergoing trials in Florida, and involve the application of acute bleaching stress and/or the rearing of corals under chronic nonbleaching stress as means of modifying symbiont communities (Andrew Baker, personal communication).

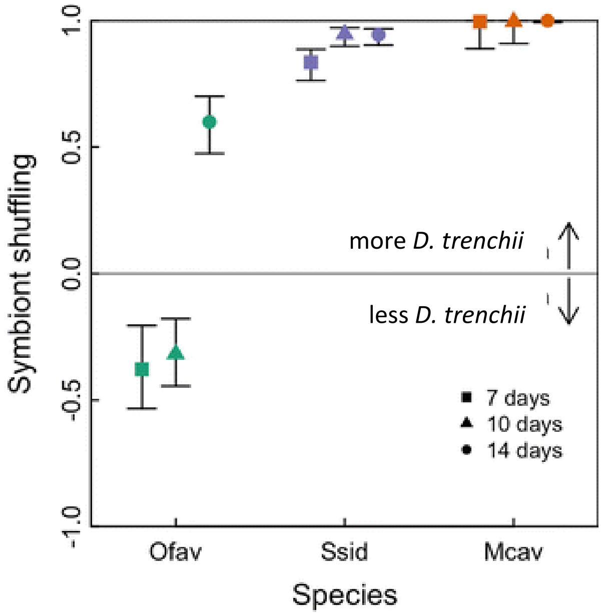

FIGURE 3.2 Relative magnitude of symbiont shuffling in the laboratory for *Orbicella faveolata* (Of), *Siderastrea siderea* (Ss), and *Montastraea cavernosa* (Mc) after recovery from 7, 10, and 14 days of bleaching induced by exposure to 32°C. The symbiont shuffling metric ranges from −1 (complete loss of *D. trenchii*) to 1 (complete dominance by *D. trenchii*), with 0 indicating no change in amount of *D. trenchii*. SOURCE: Modified from Cunning et al., 2018.

Coral recruits: The majority of scleractinian coral species (approximately 85%), including most broadcast spawners, produce gametes that do not contain algal symbionts. These species must by necessity acquire Symbiodiniaceae from environmental sources (horizontal transmission). A minority of species (approximately 15%) contain symbionts in their eggs, and these symbionts are considered maternally supplied (vertical transmission). A very few species exhibit both strategies (Baird et al., 2009a; Babcock and Heyward, 1986; Fadlallah, 1983; Harrison and Wallace, 1990). Consequently, for the majority of species, algal symbionts must be obtained *de novo* each generation, at the larval or early recruit stage, and this represents a clear opportunity for intervention. This is particularly true because the specificity of coral species for particular Symbiodiniaceae appears to be much lower in early life history stages than it is in the adult, although there is considerable variation among corals species and these systems still remain far from "open" (Poland and Coffroth, 2017; Quigley et al., 2016, 2017). Coral larvae or juveniles typically acquire diverse symbiont assemblages which are then "winnowed" during early ontogeny to a dominant symbiont (or, occasionally, subset of symbionts) that is more typical of the adult, which may itself be dependent on the prevailing environmental conditions (Abrego et al., 2009; Coffroth et al., 2001, 2006; Dunn and Weis, 2009).

The natural predisposition of most, if not all, coral larvae or juveniles to acquire algal symbionts from environmental sources (LaJeunesse et al., 2004, 2010a) suggests they could be intentionally infected with algal symbionts that have phenotypes of interest, such as high thermotolerance. This could be achieved using either lab- or field-raised recruits (Quigley et al., 2018b). Such symbionts could be naturally occurring (Little et al., 2004), selected for in the laboratory (Chakravarti et al., 2017; Chakravarti and van Oppen, 2018), or genetically manipulated (see Genetic Manipulation in Chapter 2). In fact, early life history stages are likely the most effective way of effecting changes in symbiont communities, because these stages are predisposed to symbiont acquisition and are already aposymbiotic (symbiont-free), which means that existing communities of symbionts need not be displaced or outcompeted in order for others to become dominant, as is the case with adult corals. In fact, the window during which symbionts may be readily acquired may persist for several months (Abrego et al., 2009; Boulotte et al., 2016; McIlroy and Coffroth, 2017) and likely continues into adulthood (Coffroth et al., 2010; Lewis and Coffroth, 2004). Indeed, it seems likely that symbiont acquisition from environmental sources occurs throughout a coral's life cycle, but is simply difficult to detect or conclusively demonstrate due to the large population sizes of symbionts in adult corals, and because it is almost impossible to determine with certainty whether novel symbionts are acquired from environmental sources or were simply present at low abundance somewhere in the colony beforehand.

Directed laboratory selection: Chakravarti et al. (2017) artificially selected for higher thermotolerance in *C. goreaui* (formerly *Symbiodinium* C1) symbionts over 80 generations (2.5 years) using laboratory incubators. They employed a ratchet design, in which temperatures were increased in stepwise increments, with cells showing growth at each temperature being used to seed cultures at the next higher temperature. The evolved symbionts were then used to infect *Acropora* recruits and assess their effects on growth and bleaching severity under thermal stress. These methods were generally able to select for symbionts with improved photochemical performance and higher growth rates when cultured at elevated temperatures (31^{o}C), but the increased thermotolerance acquired when free-living was less apparent in symbiosis with the coral host. In a follow-up experiment, Chakravarti and van Oppen (2018) showed that similar methods could be used to select for thermal tolerance in a variety of different genera within the Symbiodiniaceae (former *Symbiodinium* types A3c, F1, and G3) over the course of approximately 1 year (41-69 generations) but were not successful in increasing the thermotolerance of (normally already thermotolerant) *Durusdinium*. Future work is likely to focus on whether artificial selection for positive cell growth rates necessarily translates to higher bleaching resistance, and on the longevity of the increased thermotolerance once the selective pressure is removed. Regardless, the practical considerations of manipulating corals using experimentally evolved symbionts, particularly during the early life history stages, are similar whether the symbionts are naturally occurring or experimentally evolved.

Current Feasibility

Adult corals: For adult corals, the principal feasibility concerns are related to effective scaling. Laboratory bleaching is feasible, but unlikely to be practical given the need to manipulate large numbers of corals. Symbiont manipulations might be included as part of restoration efforts involving the asexual propagation of adult corals in nurseries, because significant time is already being invested in fragmenting, propagating, and outplanting individual fragments. Treatments designed to modify algal symbiont communities might be incorporated into the design or placement of nurseries and/or growout practices. For example, corals could be bleached in the field by exposing them in the short-term to high doses of solar irradiance or high-temperature stress just prior to outplanting (e.g., extremely shallow depths or reef-flat environments), and in fact such practices are currently being trialed in both the laboratory and the field in Florida (Andrew Baker, personal communication). Alternatively, nurseries could be established in locations where the environmental conditions might be expected to favor particular symbionts even in the absence of bleaching. The success of these methods in changing symbiont communities will likely depend on the coral species used, and on the environmental characteristics of the nurseries and/or outplant sites. Even if successful in changing symbionts, these approaches will still require an extra step in the restoration process, and their large-scale adoption by restoration practitioners will be more likely if the benefits of these manipulated symbiont communities are readily apparent, such as by a significant reduction in bleaching mortality.

Coral recruits: Manipulation of the early life stages of corals to introduce particular symbiont types is possible with existing technology and methodology. In fact, the deliberate infection of coral juveniles with particular symbionts, followed by outplanting to natural reef environments, has already occurred on the Great Barrier Reef (albeit as part of a small-scale experiment, rather than a large-scale intervention strategy; Little et al., 2004). The application of these methods may not yet be feasible in areas where successful recruitment is limited by other biotic or abiotic factors, such as Florida and parts of the Caribbean. However, given the interest in developing methods for improving recruitment in these areas, this approach seems poised for potential inclusion into these methods as and when they are implemented.

Potential Scale

Adult corals: Symbiont manipulations operate at the scale of the individual coral colony, and are thus subject to significant scaling limitations. However, as colonies containing manipulated symbionts are introduced to reefs, this could increase the local availability of these symbionts on reefs over time. New recruits to these reefs might benefit from the increased availability of thermotolerant symbionts, which may also become more common as temperatures increase and/or bleaching events become more frequent and severe. Similarly, adult colonies already present on the reef might also benefit from higher symbiont availability under these conditions. Consequently, there may be potential positive feedbacks that operate at the level of the individual reef that could increase the long-term effectiveness of these approaches. However, these feedbacks are largely uninvestigated from a research perspective.

Coral recruits: Scaling limitations are slightly alleviated for coral recruits, due to the high numbers of recruits that could be treated with preferential symbionts during an *ex situ* rearing or grow-out phase. Although this method still operates at the level of the individual, the small size of recruits, and the large numbers that are typically produced during a spawning event mean that such interventions might be scaled up as part of a managed breeding approach.

The long-term fate of these symbionts in corals is likely to depend on the environmental conditions at the restoration site, with warmer conditions naturally favoring thermolerant symbionts, and cooler conditions favoring thermosensitive symbionts (LaJeunesse et al., 2009) that translocate more photosynthate (Cumbo et al., 2018). Consequently, the long-term value of introduced symbionts will depend critically on the future environmental conditions at the site of interest, and on the coral species of interest. Infected corals must maintain at least some of these symbionts over long time scales (probably at least several years), and these symbionts must have value in increasing resilience to the intended stressor, such as thermal bleaching. However, there have been very few studies on the longevity of these associations in the field, where coral recruits were specifically infected with particular symbionts (in the laboratory or other *ex-situ* facility) and then outplanted to the reef. Little et al. (2004) showed that *Acropora* recruits experimentally infected with different symbionts maintained these symbionts for at least 6 months on the reef, using symbionts that are commonly found in these corals. In contrast, Coffroth et al. (2010) successfully infected bleached *Porites* with symbionts that included types that did not normally associate with these corals, but found that infected corals reverted to their typical associations after 5 weeks. Therefore, the risk of symbiont manipulations failing is highly dependent on the identities of both the host and symbiont.

Risks

The manipulation of algal symbiont communities in favor of particular traits (such as higher thermotolerance) is likely to be accompanied by tradeoffs, regardless of how these symbionts are obtained (through isolation and culture, experimental evolution, or transgenic modification). Symbionts that are naturally more thermotolerant, such as some members of *Durusdinium*, impart greater thermal tolerance to their coral hosts but grow more slowly (Little et al., 2004; Jones et al., 2008; Jones and Berkelmans, 2010; Pettay et al., 2015), likely because they translocate less photosynthetically fixed carbon (Cantin et al., 2009). This suggests that increases in heat-tolerant symbionts may lead to slower-growing reefs, with implications for the reefs' ability to maintain coral-dominated states or growth rates that keep up with sea-level rise (Ortiz et al., 2013). However, this tradeoff has also been shown to be temperature-dependent (at least for *D. glynnii*), with the reduction in coral growth rate associated with *D. glynnii* decreasing and eventually disappearing at warmer temperatures (Cunning et al., 2015b). Consequently, the benefit of increased survivorship relative to reduced growth is likely to be dependent on the temperature regime at the site of interest. This is also likely true for other tradeoffs associated with the thermotolerance, for example, impacts on host reproductive output and disease susceptibility. However, both positive and negative effects of *Durusdinium* have been documented on host reproduction (Jones and Berkelmans, 2010; Winter, 2017) and disease susceptibility (Correa et al., 2009), and these different findings likely reflect significant interactions between bleaching and both disease and growth. In bleaching years, corals hosting *Durusdinium* may bleach less severely and consequently grow faster and have less disease compared to corals that do not host *Durusdinium*. However, in nonbleaching years these patterns may be reversed. As before, the changing environmental conditions are likely to determine to relative costs and benefits of having different symbionts.

Tradeoffs in experimentally evolved Symbiodiniaceae are also likely to exist, although they have not been conclusively demonstrated to date (Chakravarti et al., 2017; Chakravarti and van Oppen, 2018). Instead, some of the risks associated with the use of experimental evolution are likely to be more similar to those outlined in Managed Selection and Managed Breeding in Chapter 2, in which selection for one trait may come at the expense of others, or local genetic variation is lost. For example, artificial selection for thermotolerance (in this case through mutations accumulated during asexual reproduction of cultures in incubators) might disrupt adaptation to other factors not related to high temperature. Additionally, certain genetic risks of field introductions, such as hybridization with native symbionts as a result of sexual reproduction in the free-living state, leading to outbreeding depression, may be more of a concern for interventions involving experimentally evolved symbionts than they might be for naturally occurring symbionts.

Finally, it has also been suggested that *D. trenchii*, first described as an “opportunist” by LaJeunesse et al. (2009), might actually be an invasive species from the Indo-Pacific that has spread rapidly through a variety of Caribbean hosts at numerous sites (Pettay et al., 2015). This points to uncertainty in our understanding of the changing symbiotic milieu on coral reefs (Pettay et al., 2015; Stat and Gates, 2011): do changes in *D. trenchii* represent a mechanism that may allow some corals to persist through bleaching events and therefore ultimately prove beneficial given the current climate change crisis (Baker et al., 2004, 2008; Baskett et al., 2009), or are they invasive opportunists whose overall effects, including reductions in coral calcification rate, are deleterious even under climate change scenarios (Ortiz et al., 2013; Pettay et al., 2015)? These questions continue to be areas of active research.

Limitations

In addition to potential tradeoffs, the degree to which symbiont manipulations might be utilized as part of an intervention might be limited by a variety of other factors:

(1) *Specificity and flexibility.* At the fundamental level, these interventions depend on the extent to which different symbionts are functionally different from one another (Suggett et al., 2017) and the degree to which different coral species are able to form stable associations with other symbiont types, in particular thermotolerant varieties (Baker, 2003; Cunning et al., 2018). Dynamic changes within individual colonies appear to be common among species that routinely host multiple types (Rowan et al., 1997; Baker 2001; Berkelmans and van Oppen, 2006; LaJeunesse et al., 2009; Grottoli et al., 2014; Silverstein et al., 2015, 2017; Cunning et al., 2015a, 2018). But it remains unclear whether symbiont manipulation is limited to particular coral species that are unusually flexible. Other species may be far less labile in their associations, severely limiting the utility of this intervention. One way of overcoming this limitation is to apply directed laboratory evolution to symbionts that are already found in the coral host of interest (Chakravarti et al., 2017; Chakravarti and van Oppen, 2018). However, it is not yet clear

whether evolved symbionts with higher thermotolerance necessarily result in corals that have greater resistance to coral bleaching.

(2) *Longevity*. New symbionts may be lost over time (LaJeunesse et al., 2010b; Thornhill et al., 2006a, 2006b) or experimentally evolved symbionts (Chakravarti et al., 2017; Chakravarti and van Oppen, 2018) may lose their evolved thermotolerance. Both of these processes are likely dependent on the thermal regime at site of interest.

(3) *Availability*. The capacity of corals to undergo changes in symbionts, especially as a result of controlled bleaching and recovery, may be dependent on the local availability of appropriate symbiont; it may be easier to stress-harden corals in some places than others. There is also extreme symbiotic complexity at some sites (e.g., Mexico; Kemp et al., 2014) but not others (e.g., Bahamas; Thornhill et al., 2006b; see also Kennedy et al., 2015, 2017). It is clear that *D. trenchii* is present throughout the Caribbean in at least some hosts (*O. annularis*), with varying levels of abundance ranging from trace background levels to virtual dominance (Kennedy et al., 2015). It appears that *D. trenchii* is increasing in abundance throughout the region, and these increases are likely due to environmental conditions and in particular chronic thermal stress (Kennedy et al., 2017). However, an appropriate long-term study has not yet been undertaken.

Infrastructure

The cost of symbiont manipulations, and the infrastructure (personnel, facilities) needed, are dependent on how well these activities are integrated into existing coral restoration activities (either asexual or sexual) at the site of interest. If effectively integrated into an asexual restoration program involving coral nurseries and outplanting, costs might be low to implement once a prescriptive bleaching protocol has been developed, or a chronically warm nursery site identified. Costs are likely to be even lower to incorporate symbiont manipulations into a sexual restoration program involving larval rearing and assisted recruitment. In fact, the potential benefits and ease of introducing algal symbionts during coral early life stages are such that failing to incorporate such measures would probably represent a lost opportunity

MICROBIOME MANIPULATION

What It Is

This section will highlight the current body of knowledge regarding studies undertaken to manipulate the microbiome of corals for building coral resilience. The microbiome in this context is excluding the photosymbiotic dinoflagellates and relatives (manipulation of which is described in the previous section), but includes the fungal, prokaryotic (bacteria and archaea), and viral components of the microbiome. Peixoto et al. (2017) proposed the term Beneficial Microorganisms for Corals (BMCs) to refer to specific microbial symbionts that promote coral health. The proposed mechanisms by which the BMCs can influence host coral health include facilitation of enhanced nutrient cycling, biological control of potential pathogens, supply of essential trace nutrients, metals and vitamins plus provision of stress regulators (such as catalase and superoxide dismutase) which mitigate reactive oxygen species (ROS) within the coral holobiont (Bourne et al., 2016; Peixoto et al., 2017). Through augmentation of the beneficial native microorganisms associated with coral, stress response and tolerance mechanisms may be enhanced. However, while the diversity has been assessed extensively (reviewed in Bourne et al., 2016; Huggett and Apprill, 2018), very little is known about the functional attributes of the coral microbiome.

Coral-associated bacterial diversity has been shown to depend on environmental habitat and surrounding environmental conditions (Hong et al., 2009; Littman et al., 2009; Rohwer et al., 2002). Ziegler et al. (2017) recently suggested that coral heat tolerance was causally linked with the associated bacterial community, reporting that corals exposed to different thermal regimes harbored different microbiomes. Importantly, for reciprocally transplanted corals, the microbiomes of corals from stable cooler environments shifted during bleaching conditions while the microbiomes of corals from variable warmer climes, also exposed to bleaching conditions, showed no community shifts, suggesting a role of the microbiome in the response of corals to the heat stress (Ziegler et al., 2017). However, it cannot be determined from this study if the microbiome directly influences host thermal resilience. For other related cnidarian model taxa such as *Nematostella vectensis* (starlet sea anemone), the fine-scale microbial community composition has been proposed to influence the hosts' ability to acclimate or even adapt to changing environmental conditions (Mortzfeld et al., 2016).

Microbes occupy a variety of niches within the coral holobiont, and the ability to manipulate them for coral resilience depends on knowledge of their function and composition across these niches.

(1) Microbial communities in the external nutrient-rich **mucus layer** are likely influenced by the external environmental conditions surrounding the holobiont, as well as by the exudates from the corals, and are likely to be highly diverse (Bourne and Webster, 2013). In model systems such as *Hydra*, the bacterial communities residing in this mucus layer are structured and actively cultivated by the host, providing a vital function that supports the host health (Deines and Bosch, 2016; Augustin et al., 2017), although it is unclear if coral can do the same.

(2) Within the **tissues** of corals, the microbiome is much less diverse and highly organized within bacteriocytes that have been termed coral-associated microbial aggregates (Work and Aeby, 2014). One common bacterial taxon associated with corals (and a range of other marine invertebrates) is the *Endozoicomonas* genus (Bayer et al., 2013; Neave et al., 2017b). A number of studies that have stressed corals documented a shift in the microbiome, with a reduction in the relative abundance of *Endozoicomonas* communities associated with healthy corals to microbial communities that are characterized by opportunistic species such as those of the family Rhodobacteraceae (Cardenas et al., 2012; Pollock et al., 2017a; Roder et al., 2014; Sunagawa et al., 2009).

(3) The **skeleton** of corals also contains a diverse and distinct microbiome compared to the other niche environments of the coral holobiont (Bourne et al., 2016). This endolithic community can be very different depending on the morphology of the corals (i.e., mounds verses branches) and it is often a mix of eukaryotic algal, fungal, and bacterial communities (Marcelino et al., 2017). Only recently have studies documented the taxonomy and functional attributes of some of these endolithic communities (Yang et al., 2016). It is currently unknown what role if any this microbial endolithic community has in supporting the overlying tissues and the coral holobiont in general. Fine and Loya

(2002) looked at bleached corals and demonstrated that during bleaching, the endolithic community bloomed and provided additional nutritional supplementation to the coral tissues.

(4) The **gastric vascular cavity and coelenteron** fluid that connects coral polyps through the coenosarc region has been proposed to contain a unique and diverse microbial community that can be influenced by water flow and heterotrophic feeding of the coral polyps (Agostini et al., 2012; Bourne et al., 2016). The bacterial communities in the gastric cavity have been demonstrated to be high in vitamin B12 and hence provide important trace nutrients to the coral holobiont (Agostini et al., 2009).

Benefit and Goals

Microorganisms are central to their host's physiology, contributing across a range of functions from immune systems, development pathways, and behavior (Bosch and McFall-Ngai, 2011). The microbiome can respond rapidly to the surrounding environment often through rapid adaptive evolution (Elena and Lenski, 2003) and, hence, is suggested to be a powerful influence on coral acclimation and even adaption to rapid anthropogenic driven changes and/or disturbance (Webster and Reusch, 2017). This potential for coral-associated microorganisms to be a driver of adaptive coral host responses is due to their high abundance, their large diversity (both taxonomically and functionally), and their short generation times (Torda et al., 2017). By shifting the microbiome or changing the relative abundance of functionally important groups, the phenotype of the coral host and subsequently its response to environmental change may be shifted, a process termed microbiome-mediated acclimatization (Webster and Reusch, 2017). The hologenome theory of evolution proposed that microbiome-mediated processes that change host fitness can be under selective pressures (Rosenberg and Zilber-Rosenberg, 2013), although the theory has sparked widespread debate and much controversy (Bordenstein and Theis, 2015; Moran and Sloan, 2015). Many reef invertebrates engage in vertical transmission of their microbial symbionts, facilitating microbiome-mediated transgenerational acclimatization if it also confers lasting adaptive benefits to the coral host (van Oppen et al., 2015a). Hence, through manipulation of the coral microbiome (i.e., changes in abundance and/or addition of new members), the resilience of corals to changing environments may be increased for existing coral populations, including a wide range of native species and genotypes, and potentially passed on to future generations.

How to Do It

There are a number of approaches that can be taken to manipulate the coral microbiome with the aim of improving the resilience of the coral host to environmental stress. Different approaches to manipulate the microbiome of corals may include the following:

(1) Shifting the abundance of the existing (native) coral microbiome populations through isolation and addition of these native communities to the coral holobiont;
(2) Addition of new bacterial populations that have functions beneficial to the coral holobiont (which might not be derived from the reef environment);
(3) Subjecting the coral holobiont to environmental stress to promote selection of microbiome members that may have adaptive traits to confer benefits to the coral host (see Pre-exposure earlier in this chapter); and

(4) Applying genetic engineering approaches (transposon/CRISPR-Cas9 systems) to introduce traits in bacteria that are beneficial to coral fitness (i.e., increased ROS scavenging capabilities), and addition of these modified microbial populations into the corals' normal microbiome (see Genetic Manipulation in Chapter 2).

Examples to date of coral microbiome manipulations and their resulting effects on the coral host are described here:

- Santos et al. (2015) selectively isolated coral-associated bacterial strains capable of degrading water-soluble oil fractions and re-added these strains to corals before exposing them to conditions that simulated an oil spill. Corals exposed to the bacterial additions displayed higher symbiont photosynthetic competence compared to coral treatments without the added bacteria, indicating improved health outcomes.
- Damjanovic et al. (2017) exposed *Acropora tenuis* larvae to coral-derived microbially laden mucus from different species (*Acropora sarmentosa*, *Acropora tenuis*, *Diploastrea heliopora,* and *Galaxea astreata*). After subsequent rearing of the larvae for 4 months, the microbial communities associated with *A. tenuis* juveniles differed across all initial mucus addition treatments. These preliminary studies indicated that just one addition of a mucus/microbial cocktail could shift the coral-associated microbiome during early ontogeny, although no information is available on if or how the microbial communities influenced coral health/fitness.
- Welsh and Vega Thurber (2016) isolated the predatory bacterium *Halobacteriovorax* from the coral microbiome and showed it could regulate the coral-associated microbial communities through top-down control of certain bacterial species. When added to corals that had also been challenged with the coral pathogen *Vibrio coralliilyticus,* the predatory bacterium ameliorated changes in the coral microbiome and prevented secondary colonization of opportunistic bacterial groups identified as indicators in compromised coral health (see also Welsh et al., 2016, 2017).
- BMC cocktails have been developed through isolation of a range of bacterial species that displayed potential beneficial traits for corals including nitrogen fixation and/or denitrification, dimethylsufopropionate degradation, or antagonist activity against putative bacterial pathogens. The BMC cocktail was added to corals in aquariums that were subjected to heat stress to simulate a bleaching event as well as bacterial challenge with the coral pathogen *Vibrio coralliilyticus*. BMC-inoculated corals displayed improved health compared to noninoculated controls through lower bleaching metrics, demonstrating the potential for addition of BMCs to minimize the impacts of environmental stressors (Raquel Peixoto, personal communication).

Current Feasibility

Approaches to manipulate the coral microbiome are currently feasible at the small experimental scale. Investigated approaches have currently only shown that shifting of the coral host microbiome is possible (Damjanovic et al., 2017) or have demonstrated that addition of microbial isolates is correlated to an improved outcome for the coral host under stress conditions (Santos et al., 2015; Welsh and Vega Thurber, 2016; Ziegler et al., 2017). How the microbiome is shifted at the cellular level and by which mechanisms these benefits are conferred is still currently not understood. The longer-term effects, including whether the shifted microbiome is stable and provides continued benefits to the coral host or if other negative tradeoffs occur is not known.

The approach is also feasible at the level of whole aquarium/grow-out facilities. Like other animal production systems, development of microbial probiotic cocktails that provide benefits to corals is feasible. However, there is much research to be conducted to deduce which microbes are beneficial and at what abundance, and how they can be administered to shift the coral microbiome to increase fitness of the holobiont. These unknowns make it unlikely that benefits will be seen at the reef scales in the near term, but development of improved coral diets that include probiotics, and ways to manipulate the coral microbiome that promote environmental resilience, is potentially achievable with extensive research and development.

Potential Scale

The coral-associated microbiome is generally specific for coral species and even across populations of one species. Hence, approaches aimed at shifting the microbiome are likely required for each specific site and target species (Peixoto et al., 2017). This has applicability for experimental work but also for coral aquariums that may be looking to enhance resilience of corals to be introduced back into the field for restoration.

Inoculation of BMCs could be feasible at reef scales through approaches such as microencapsulation of beneficial microorganisms into “coral food packets” that can be spread onto reefs. Mass production of probiotics exists in both human and animal health fields. However, what is not evaluated or feasible currently is the specific delivery of BMCs into the coral coelenteron. The efficacy of this approach in modulating the coral physiological response to environmental conditions is unknown. Additionlly, the delivery systems that could manipulate the microbiome of the target coral species with the desired microbial cocktail specifically, economically, and with minimum risks have not been developed.

On a temporal scale, addition of BMCs could be applied at early and peak periods of environmental stress to minimize physiological impacts, and potentially even following the stress events to help coral recovery. The timing of the addition of microbes to build resilience would be dependent on effectiveness and at what stage in development/growth of corals the microbiome can be modified and if the modified microbiome can be maintained.

Risks

The risks associated with manipulation of the coral microbiome depend on the approach taken. Shifting the relative abundance of naturally occurring (“native”) coral microbiome populations likely represents a relatively small risk as this form of augmentation is minimally invasive and aims to preserve the native microbiome diversity in the reef. However, introduction of high numbers of “foreign” microbes with putative beneficial effects for the coral may drive other unintended processes, including changing pathways of nutrient flow within the coral colony itself or on reefs more generally or introduction of putative pathogens for other reef-based organisms. On the other end of the spectrum, introduction of genetically modified bacterial taxa with engineered benefits for the coral host (such as enhanced ROS scavenging) is associated with many risks requiring full evaluation (see the discussion in Chapter 2 on Genetic Manipulation).

Shifting the microbiome partners may also result in tradeoffs similar to those possible when shifting algal symbionts (i.e., confering thermal resilience but with reduced growth). However, there currently is no information regarding what the tradeoffs may be. Current studies indicate that certain coral-associated bacterial taxa are closely associated with many corals (i.e., Endozoicomonas family); however, under times of stress, these microbial groups decrease in relative abundance in healthy coral and other taxa (i.e., Rhodobacteraceae family) increase in relative abundance (Cardenas et al., 2012; Pollock et al., 2017a; Roder et al., 2014; Sunagawa et al., 2009). This maybe an incidental rather than direct effect of declining coral health, but such taxa can be used as indicators of coral health when looking at tradeoffs (Glasl et al., 2017).

There is also a risk of propagating, incubating, and releasing microbial pathogens into the open reef systems. Disease in any population is always an interaction between the host, the environment, and the causative agent (Wobeser, 2007). In artificial propagation systems, disease is more problematic when there is suboptimal environmental conditions (which can promote pathogen growth and reduce host immune function) and a high host population density (Harvell et al., 2009). Hence, disease management and quarantine operating procedures need to be optimized to reduce risks of unintended spread of disease into native populations (Sweet et al., 2017). In addition, any added or manipulated members of the coral microbiome would need to be extensively tested to ensure they do not represent disease agents for other-coral reef-inhabiting animals.

Limitations

Currently there is limited knowledge regarding what shapes and maintains the coral microbiome and how the microbiome can be shifted for the benefit of coral fitness, but it is an active field of research. Despite an extensive body of research focused on the diversity of the coral microbiome, few studies have specifically identified the functional attributes individual members of the microbiome provide to the coral host. At present, any microbiome manipulation takes a black box approach. It is assumed that an observed benefit to coral host physiology when adding a microbial cocktail is due to the direct effects of the microbial community. However, the mechanisms at the cellular level that influence the coral hosts' physiology are unknown and could be due to indirect effects. For example, just adding a microbial cocktail could provide a nutritional component that may enhance the corals physiological resilience. Any mechanistic understanding of the influence of microbiome manipulation on coral physiology would need to resolve which niche the beneficial microbes occupy (i.e., mucus, tissue specific, coelenteron, or skeleton microbial communities).Therefore, understanding the interactions of the members of the coral holobiont at the cellular level is critical to ensure any microbiome manipulation is directly facilitating improved coral fitness and resilience.

These limitations also are influenced by limited knowledge on the most effective approaches for delivering and shifting microorganisms to facilitate higher fitness. For example, increasing the abundance of a known microbial ROS scavenger may have little positive influence if the site of colonization of the microorganism is removed from the sites of ROS production within the coral.

It is also unknown whether introduced microbial communities remain associated with corals and influence coral fitness traits over extended periods or into the next generation of corals. There are studies currently focused on transgenerational effects of microbial symbionts on reef invertebrates under future climate scenarios, though the outcomes of these studies are still a work in progress (David Bourne personal communication). The longer-term effects of shifting the microbiome may not be central if looking at just buffering coral resilience through a single stress event such as a bleaching period, however if looking to enhance population tolerance over longer time frames then the question of persistence of the microbiome needs to be considered.

Infrastructure

Infrastructure needs associated with coral microbiome manipulation are principally associated with research and development, specifically in areas of isolation and identification of beneficial microorganisms and testing their efficacy in small-scale aquarium trials. This is due to limited understanding of the specific function of members of the microbiome, how to manipulate them, and if manipulation can be linked to improved outcomes for the coral host. If suitable microbial cocktails are identified and developed, the next steps would be to integrate them into coral nurseries and outplanting sites, taking advantage of the infrastructure established for propagating corals. At these small scales, the costs would not be extensive and application would take advantage of technological applications in other fields such as agriculture and food production, that currently implement probiotics or microbiome manipulation to boost production. Effective delivery of the microbiome needs to be developed and may take the form of microencapsulation for formulation of coral diets that deliver probiotics/BMCs into corals. These approaches are well developed in other industries and cost effective at limited scale, though, as highlighted previously, the desired specificity and efficacy of these delivery mechanisms does not currently exist. When considering manipulation of the microbiome at large reef scales, there are many unknowns, and infrastructure requirements and costs will no doubt subsequently increase. While industrial production of microbial cocktails is feasible, effective delivery at such large scales has not been currently not explored.

ANTIBIOTICS

What It Is

Antibiotics (also known as antibacterials) have found widespread use (and overuse) in the treatment and prevention of bacterial infections in human, animals, and agricultural systems (Allen, 2017; Chang et al., 2015). Antibiotics can be highly effective in the prevention and treatment of bacterial (and some protozoan) diseases. In combination with ease of access to large quantities and cheap cost of production, they can be highly beneficial to many applications spanning human health and large-scale animal production, including valuable marine aquaculture target species (Topp et al., 2017).

Benefit and Goals

Where corals are already displaying signs of stress or disease, therapeutic approaches can improve the health of the individual coral or the reef ecosystem as a whole. Improvements in corals' condition through antibiotics (or other therapeutic approaches) might thereafter increase their resilience to environmental stress. In the best-case scenarios therapeutic approaches may even cure that individual or population from impairment in function, for example in a disease outbreak.

Marine diseases are on the rise globally and coral diseases continue to be reported across ocean basins (Burge et al., 2014; Harvell et al., 2004). In the Caribbean, coral disease resulted in mass mortality of many species through the 1980s and 1990s, with these outbreaks decimating the important reef-building branching *Acropora* species (*A. palmata* and *A. cervicornis*) specifically (Aronson and Precht, 2001b), as well as the critically important herbivore *Diadema antillarum* (Lessios, 2016). A number of bacterial causative agents were implicated in some of the disease outbreaks, although definitive links between the causative agent and the disease lesion is still lacking in many cases (Work et al., 2008). Despite much debate on the causation of diseases (Mera and Bourne, 2018), antibiotic treatment can represent one treatment option to arrest disease spread.

How to Do It

Application of antibiotics could conceivably be used under two scenarios:

(1) At the localized interface of disease lesions with healthy coral during a field-based disease outbreak. A successful treatment of black band disease, for example, was implemented using an aspirator device to remove the microbial mat that infected the colony (Hudson, 2000). Subsequently, a modeling clay sealant was pressed into the coral skeleton at the site post-aspiration, reducing reinfection. Inclusion of an antibiotic cocktail into the sealant clay may represent a viable application that improves effectiveness of this dedicated treatment. Experimental trials are lacking in this area and therefore further investigations would be needed to assess applicability, effectiveness, and scalability.

(2) Many aquaculture facilities historically have integrated broad-scale antibiotic treatment into rearing processes when disease outbreaks crippled production (Topp et al., 2017). Applications of antibiotics in coral husbandry and rearing facilities can also be undertaken as a preventative approach to mitigate potential future disease outbreaks. With coral nurseries currently being established at many sites around the world and the growing need for restoration of reef ecosystems, the planned growth of large scale *in situ* and *ex situ* coral nurseries is inevitable (Rinkevich, 2005). Within the coral hobby aquarium field, antibiotic treatments are commonly applied and sometime actively promoted across websites and in grey literature publications (Sweet et al., 2011; Sheridan et al., 2013). Often this has involved dosing of the antibiotic into the surrounding water, or removing individual colonies from the tanks and dipping them in an antibiotic bath before placing back into the tanks.

Current Feasibility

Application of antibiotics is feasible currently when applied at small scales either via direct application to individual coral colonies in the field or at the scale of the hobbyist aquariums (Sweet et al., 2011). Larger-scale aquaculture facilities routinely apply antibiotics to high-value marine seafood target species, although the actual figures and efficacy of such approaches can be questioned (Allen, 2017; Watts et al., 2017). Such approaches and operating procedures are similarly applicable to coral aquaculture and propagation facilities.

Potential Scale

Application of antibiotics *in situ* on coral reefs can be highly contentious, although it is feasible when applied at the scale of treating individual coral colonies. This approach is labor intensive and most efficiently applied in areas that have detailed information on the prevalence of the disease outbreak within the coral population, indicating where individual coral colonies can be targeted to potentially reduce the risk of disease spread. This approach is currently being tried in sections of the Florida Reef Tract where a disease outbreak in recent years has decimated remnant coral colony populations (Erinn Muller, presentation to committee). In this case, an antibiotic cocktail sealant has been added at the lesion interface to prevent progression of the disease, similar to the approaches tried by Hudson (2000). Application of antibiotics more broadly and diffusely in open coral reef systems including *in situ* nurseries to enhance resilience of corals to disease outbreaks is feasible, although the effectiveness of such an approach has not been established and is questionable due to dilution effects, the potential for the spread of antibiotic resistance (discussed below), and other potential unknown impacts.

Application of antibiotics to corals within closed research facilities and larger closed nursery propagation systems is feasible. In experimental systems, the addition of broad-spectrum antibiotics such as ampicillin has been successful in enhancing coral larva settlement and survival, potentially through reduction in antagonistic microbial populations stimulated via algal exudates or lowering coral resistance to microbial infections (Vermeij et al., 2009). The application of antibiotics is still prevalent in many high-value marine aquaculture facilities globally (Allen, 2017; Topp et al., 2017; Watts et al., 2017) and therefore available dosing protocols, supply, and cost all make antibiotic treatment to prevent disease within closed coral systems feasible on this scale. Most published studies that have used antibiotic treatment on coral, though, have focused on testing causative agents. For example, Sweet et al. (2014) applied ampicillin and paromomycin to Caribbean *Acropora cervicornis* corals, which arrested the advancing white band disease type 1 lesions. In studies such as this, treatment is within closed aquarium systems, at very small scale, generally focused on elucidating specific questions around causation and causative agents of disease (Sweet et al., 2014), and not targeted or promoted as therapeutic approaches to improve coral resilience.

Temporal scales also need to be considered when using antibiotics. Often antibiotics have short half-lives and are sensitive to light and temperature. This, along with the rapid dilution of the antibiotics in both closed and open systems, make repeated addition of antibiotics required to arrest disease progression. This contributes to issues such as the rise of antibiotic resistance in target and ancillary microbial populations.

Risks

The inherent risks associated with widespread and rampant use of antibiotics are widely acknowledged in agricultural and human systems (Larsson et al., 2018; Topp et al., 2017). The primary risk is spread of antibiotic resistance through microbial populations that leads current antibiotics to become useless for target organisms (Larsson et al., 2018). Proliferation of antibiotic resistance may occur in the microbiomes of nontarget organisms exposed to the antibiotics as well.

Within the coral context specifically, antibiotic treatments may affect a range of other commensal and potentially beneficial coral-associated microbes, potentially resulting in a destabilized microbiome (dysbiosis) that may subsequently contribute to poor health outcomes for the coral host. Recent studies have highlighted how microbial dysbiosis for coral and other marine organisms is a good indicator of compromised host health (Egan and Gardiner, 2016; Zaneveld et al., 2017). Application of antibiotics, especially as a preventative measure against disease, may therefore destabilize the healthy coral microbiome, making these coral colonies more susceptible to disease. Overall, application of antibiotics and the assessment of risk with coral systems would be needed on a case-by-case basis due to concerns over antibiotic resistance and over use of antibiotics in environmental settings (Normark and Normark, 2002).

Limitations

There are many limitations related to the use of antibiotics that go beyond the identified risks of spreading antibiotic resistance. For example, in corals, a major limitation is that many causative agents of coral diseases have not been identified (Bourne et al., 2009; Mera and Bourne, 2018). This necessitates the use of broad-spectrum antibiotics, which target bacterial cellular processes that are common for many different bacterial groups, such as inhibition of cell wall structure formation (Kohanski et al., 2010). Use of such broad-spectrum antibiotics therefore results in destabilization of the beneficial microbiome in addition to targeting any coral pathogen implicated in disease. Antibiotic usage in coral systems is also limited by knowledge gaps regarding effective dosages, and delivery mechanisms across different scales, from individual colonies to individual tanks to open reef systems. Additionally, the short half-life due to light sensitivity results in the need for repeated dosing. A major limitation on the effectiveness of antibiotics is that by the time that disease is observed, administration of the antibiotic maybe too late to arrest the impacts, making application fruitless (Sweet et al., 2011).

Infrastructure

Antibiotics are readily available and cheap, and a wealth of information on delivery to terrestrial animal, agricultural, and marine aquaculture species has been developed. However, specific application to corals would require the development of technology so that benefits outweighed the risks of antibiotic application and prevent broad release into the environment.

PHAGE THERAPY

What It Is

Phage therapy is the isolation, identification, and application of viruses that specifically target and infect bacteria, known as bacteriophages or simply phages (Abedon et al., 2017). Through infection and lysis of the target bacteria, progression of bacterial-mediated diseases can be arrested (Skurnik and Strauch, 2006). Phage therapy has been a successful approach used in human medicines and was highly advanced especially in Eastern European countries prior to the widespread use of antibiotics (Abedon et al., 2017; Nobrega et al., 2015). Engineered bacteriophages are being developed for human-based trials to counter antibiotic-resistant bacteria that have emerged in the population (Doss et al., 2017).

Benefit and Goals

Today there is renewed interest in using bacteriophages to target a wide range of human disease with bacterial causative agents due to the rise of antibiotic resistance in many previously sensitive bacterial pathogens (Abedon et al., 2017; Torres-Barceló and Hochberg, 2016). There are advantages in the application of phage therapy including the quick and inexpensive preparation of a bacteriophage. In addition, bacteriophages are highly specific to the target bacterial strains making it unlikely that other symbiotic microbes of the coral holobiont are affected (unlike broad-spectrum antibiotics). The bacteriophage population also stays active in the environment that the host inhabits until that host (pathogen) population is below critical levels, meaning fewer or limited applications of the bacteriophage may be required to control the target bacterium (Abedon et al., 2017; Doss et al., 2017; Nobrega et al., 2015; Torres-Barceló and Hochberg, 2016).

How to Do It

The phage therapy approach has been applied to coral in both closed aquariums and open reef environments (Atad et al., 2012; Cohen et al., 2013; Efrony et al., 2007, 2009). The approach takes advantage of the principle that for every bacterium there are one or many bacteriophages that have evolved (or coevolved) to infect and/or lyse that bacterium (Keen, 2015). Once samples with high viral load have been cocultured with the target bacterium, any viruses infecting the bacterium will multiply, lyse the bacterium, and then be released into the surrounding medium. Through repeat enrichments, high bacteriophage concentrations can be obtained. For experimental trials, bacteria can be grown on microbial media and the bacteriophage stocks added to see which ones cause clearance of the bacterial lawn. Those that lyse the bacteria can be further purified and concentrated before identification. Once a bacteriophage is isolated and shown to be specific to the target bacterium, it can be grown in large volumes for applications ranging from small to reef scale.

Current Feasibility

Agriculture and aquaculture systems have applied phage therapy to treat plants subject to bacterial-mediated disease and high-value target marine organisms that are often subject to debilitating diseases (Doss et al., 2017). The US Food and Drug Administration has approved application of phage therapy for some crops (Doss et al., 2017). Bacteriophages targeting the putative coral pathogen *Vibrio coralliilyticu*s have been isolated and used effectively to stop advancing white plague-like lesions on *Favia favus* coral species in the Red Sea (Atad et al., 2012; Cohen et al., 2013; Efrony et al., 2007, 2009). Hence, development for marine-based coral disease systems is feasible.

Potential Scale

The approach was originally demonstrated to be effective in small-scale experimental systems (Cohen et al., 2013; Efrony et al., 2007, 2009), and has also been shown to be effective in a proof-of-concept study and applied at the reef scale where disease takes hold (Atad et al., 2012). However, the evidence for effectiveness in open-system, reef-scale applications is limited. In theory, since bacteriophages are self-generating entities, one application rather than multiple applications over time may be sufficient. If the target bacterial pathogen proliferates, the bacteriophage will also increase in number (Doss et al., 2017). However, the specific dynamics and practical requirements of temporal applications have not been assessed sufficiently for corals or reefs in general.

Risks

Bacteriophage-mediated lysis of bacterial communities drives much of the cycling of nutrients in oceanic environments (Middelboe and Brussaard, 2017; Roux et al., 2016; Worden et al., 2015), and there is extensive horizontal gene transfer across bacterial/viral lineages in all environments. The application of large numbers of a single bacteriophage to an open reef system does present risks of uncontrolled and unintentional gene transfer events occurring, which may have negative effects on both microbial and macroorganism dynamics. For example, these unintentional effects may include the collapse of bacterioplankton populations that can result in an imbalance of nutrient cycling on the reef. Once bacteriophages are released into an open marine coral reef system, their removal would be extremely challenging or near impossible.

Bacteriophages are self-replicating individuals that have the capability to evolve. Bacteriophage have the potential to spread virulence traits across target and nontarget hosts. Some studies have highlighted that virulence and antibiotic resistance genes exist in some bacteriophage genomes, with the capacity to be passed into hosts that do not have these (Doss et al., 2017; Nobrega et al., 2015). This could result in the unintentional risk of generating new pathogens within an environment. Application of lytic bacteriophages can however minimize the risks associated with incorporation of bacteriophages into host cells and enhanced exchange of genetic information.

Limitations

A limitation to phage therapy is the potential evolution of mechanisms in bacteria to counter bacteriophage infection, allowing emergence of resistance (Doss et al., 2017). Once a bacteriophage is identified and applied, its use is limited and new bacteriophages must be constantly isolated and applied to be effective over longer time scales. While cocktails of bacteriophages that target the same host can partially overcome this obstacle, resistance will eventually arise in the target bacterial population.

Similar to use of antibiotics, another limitation of this approach is the difficulty in conclusively identifying the causative agents of many coral diseases. While bacterial pathogens have been inferred as causative agents of many diseases, there is still debate and a critical lack of understanding of the primary (versus secondary) drivers of disease in corals (Mera and Bourne, 2018). This lack of understanding of the biotic and abiotic drivers of disease will hinder the development of specific bacteriophages to many of the common diseases afflicting corals.

Infrastructure

The costs and infrastructure associated with producing bacteriophage cocktails targeted against coral pathogens is mainly associated within the research and development phase, specifically the isolation and identification of the applicable bacteriophage or bacteriophage cocktails. Once identified and shown to be specific in laboratory-based efficacy trials, the costs and infrastructure required for production and application of the cocktails under small-scale controlled environments are minimal. The technology for delivering a bacteriophage cocktail to corals in open-water reef environments needs development however to establish what is feasible, specific, and effective at this scale.

ANTIOXIDANTS

What It Is

Corals in shallow reef environments reside close to their thermal tolerance and can be exposed to high incident light levels, leading to the production of excess ROS. In corals, the antioxidants superoxide dismutase, ascorbate peroxidase, and cycling of dissolved organic sulfur compounds (DMSP, DMSO, and DMS) likely have big roles in scavenging hydroxyl radicals (Deschaseaux et al., 2014). The addition of antioxidants to corals may provide short-term scavenging (i.e., elimination) of ROS produced during extreme environmental conditions. Similarly, trace metals such as iron play a role in supporting algal symbiont photosynthesis and, conceivably, their addition may prevent the photosystem breakdown that produces excess ROS (Shick et al., 2011).

Benefit and Goals

During heat-induced thermal bleaching, increased ROS production has been linked to degradation and loss of Symbiodiniaceae cells from the coral host tissues (Smith et al., 2005; Lesser, 2006). Scavenging of ROS is an important cellular process in all animals. However, during environmental stress events such as high seawater temperature periods, particularly in doldrums conditions that promote high light penetration onto reefs, the capacity of the coral holobiont to maintain homeostasis in production and scavenging of ROS becomes disrupted in favor of production (Weis et al., 2008). Heat-tolerant corals potentially enhance ROS detoxification capabilities and this trait is potentially mediated by algal symbiont cells that reorganize their ROS antioxidant network and can be acquired transgenerationally (Levin et al., 2016; Suggett et al., 2017). Enhancing antioxidant activity within the coral holobiont through treatment with ROS scavengers may mitigate environmental stress at the cellular level.

How to Do It

Application of antioxidants to corals have been trialed by Yudowski et al. (2018), who applied catechin, a plant-derived secondary metabolite and antioxidant, to heat-stressed *Porites astreoides* fragments and to the cnidarian model system *Aiptasia pallida*. They observed reduced ROS levels in host cells, which mitigated loss of algal symbionts from host tissues and prevented declines in their photosynthetic capacity. ROS-scavenging nanoparticles ($\mathrm{RNP^o}$) have also been developed for application in tumor suppression and anti-inflammation in model vertebrate organisms such as zebra fish (Vong et al., 2015, 2016) and more recently applied to coral larvae to mitigate thermally induced oxidative stress (Motone et al., 2018). $\mathrm{RNP^o}$ are of a size that prevents interference with normal cellular redox reactions, such as the electron transport chain within cells, while still allowing for scavenging of ROS and mitigation of oxidative stress (Vong et al., 2015). When $\mathrm{RNP^o}$ was added to thermally stressed *Acropora tenuis* larvae (without algal symbionts), ROS-induced oxidative stress proteins were absent compared to controls without the $\mathrm{RNP^o}$ addition. Theoretically, other antioxidants can be trialed, and would need extensive testing on positive and negative effects at the cellular and whole-colony level. The committee could not find any published studies on the efficacy of iron addition at times of high-temperature stress to mitigate the effects of coral bleaching.

Current Feasibility

Addition of antioxidants to coral to mitigate ROS production under environmental stress is currently in the very early stages of testing feasibility, using cellular assays and testing on model cnidarian (including coral) species. The understanding of the effectiveness of this approach, although promising in early studies, is also rudimentary. It is therefore not currently feasible to implement these approaches without an extensive research and development stage that documents the benefits and any negative outcomes at the cellular, whole animal, and ecosystem levels. Subsequent investigations would also need to look at how the approach could be implemented at large scales with questions around effective delivery of the ROS-scavenging antioxidants as well as other chemical additions.

Potential Scale

Currently the scale of application of antioxidants has only been tested at the colony level, and the potential for application to reef-scale processes is unknown. The efficacy of the approaches at reef scale would be highly dependent on finding an appropriate and efficient delivery method to benefit coral during times of stress and increased internal ROS production. At temporal scales, provided the approach is shown to be effective, addition of the antioxidants and other chemicals would be required during early and peak periods of environmental stress, and potentially even following the stress events to help coral recovery.

Risks

The risks are currently unknown and would need to be assessed on each identified individual antioxidant or other chemical. While many of the antioxidants are naturally produced compounds, application of high concentrations may have detrimental impacts on organismal function. Hence, for reef-scale applications, baseline ecotoxicology assessments and safe dosing guidelines (LD50s) may need to be developed for each identified compound. A study that looked at the effect of iron addition to coral showed that the growth of the algal symbiont increased, with the effect of reducing coral calcification, likely due to reduced transfer of carbon to the coral host (Ferrier-Pagès et al., 2001). Stimulation of planktonic biomass at a large scale has been proposed as a way to draw down and sequester carbon dioxide ("iron fertilization"), and the potential risks that have been identified for this approach could apply to application in coral reef environments. The risks are that phytoplankton communities may quickly dominate and can reduce oxygen levels and other essential nutrients, which would negatively affect other marine organisms and also lead to harmful algal blooms (NRC, 2015).

Limitations

Variations in responses by various coral species to the range of potential antioxidants limits knowledge on the effectiveness of a given application. The addition of catechin to control colonies that were not subjected to temperature stress during the experiments of Yudowski et al. (2018) resulted in loss of the symbionts. This indicates a potential for the antioxidant to damage normally functioning photosynthetic pathways due to the potential importance of ROS at certain levels for signaling and cellular processes. The response to catechin was also different between the coral *P. astreoides* and the sea anemone *Aiptasia pallida*. The other currently documented approach of using RNP^{o} has been designed to avoid interference with normal cellular redox reactions, though limited understanding and the early stage of development, limits its current application for mitigation of coral stress in the field. Therefore, while addition of antioxidants may seem a promising and a future feasible option, much more work is required to understand the cellular processes mitigating ROS production and related cellular dysfunctions, the responses over many other taxa, and the ability to apply specifically to coral at scales that are effective.

Infrastructure

The infrastructure associated with antioxidants to mitigate cellular stress processes is focused on the experimental research and development phases. This includes laboratory and aquarium-related facilities where the efficacy of the approach can be tested. Testing is needed at the individual coral colony scale as well as for methods for upscaling the benefit of antioxidants or other chemicals to whole reefs or corals held within husbandry facilities, for which infrastructure requirements are currently unknown.

NUTRITIONAL SUPPLEMENTATION

What It Is

Nutritional supplementation of corals with carbon and other essential nutritional elements during periodic episodes of major stress events (e.g., bleaching that impacts their metabolic competence), represents an additional novel intervention strategy. Improved nutritional status of corals can provide increased resilience when faced with environmental stress, and condition corals in the longer term to disease and other abiotic and biotic challenges. Nutritional supplementation may compensate the coral host for compromised function of the algal symbiont cells during times of environmental stress. Within aquarium systems, supplementation of corals' energy requirements through heterotrophic feeding is already an established and essential requirement to maintain health.

Benefit and Goals

Interventions that deliver greater nutritional supplementation to coral may improve their resilience during times of environmental stress by compensating for the lost energy resulting from algal symbiont dysfunction during bleaching events. The observed visual response of coral to stress is often a result of metabolic dysfunction at the cellular level, which is directly derived from disruption of the supplied essential nutritional elements (carbon, nitrogen, sulfur, phosphorus, and trace nutrients). Healthy zooxanthellae-containing corals acquire carbon both heterotrophically and photoautotrophically. Up to 60% of the corals' requirements can be derived via predation upon zooplankton, pico- and nanoplankton, dissolved organic matter, and suspended particulate matter while up to 90% can be obtained via photosynthetically fixed carbon translocated from zooxanthellae (Grottoli et al., 2006; Falkowski et al., 1984, 1993; Muscatine et al., 1981; Palardy et al., 2008). The underlying mechanisms of carbon capture within the coral holobiont are still not well understood, however, and likely differ greatly between different coral species with varying morphologies (Ferrier-Pagès et al., 2011). Recent studies have demonstrated that 70-100% of daily carbon requirements are met through heterotrophic feeding and that corals can up-regulate feeding when photosynthesis is lower (Ferrier-Pagès et al., 2011; Grottoli et al., 2006; Houlbrèque and Ferrier-Pagès, 2009; Tremblay et al., 2015). This is especially important during periods of temperature stress when algal symbionts are lost from the coral tissues and corals increase heterotrophic feeding to compensate (Palardy et al., 2008; Tremblay et al., 2016). The endolithic communities of corals have also been reported to be an important route of carbon into the coral holobiont, with blooms of endolithic algae during a coral bleaching event partially supplementing lost carbon (Fine and Loya, 2002).

How to Do It

Nutritional sources include a range of zooplankton, picoplankton, and nanoplankton. The coral aquarium trade, research facilities, and hobby aquarists routinely supplement the coral diet with a range of commercial feeds that include phytoplankton, rotifers, krill, and even pieces of shrimp, squid, or clams. However, there is currently no dedicated or robust assessment of an optimized coral diet supplementing nutrition to build coral resilience.

Current Feasibility

Nutritional supplementation of corals is mature for corals that are maintained in small-scale hobbyist tanks and larger-scale display and research aquarium facilities. Facilities that are focused on growing coral for outplanting onto reefs and that can provision the corals with the best nutritional competency will have important beneficial effects for survivorship and building resilience in coral populations. Optimized diets may also include probiotic microbial candidates (probiotic cocktails) or enhanced antioxidants that improve the fitness traits of coral. For *in situ* reef-wide applications, the approach is currently not feasible; work is required to develop improved coral-specific diets that can be delivered most efficiently for a wide number of coral taxa that can be differently constrained by polyp size and requirements of heterotrophic and autotrophic energy acquisition.

Potential Scale

The current scale of nutritional supplementation of corals is only in enclosed conditions at the hobbyist scale and small to large coral aquaculture/propagation facility levels. Operations at reef scale have not been undertaken to date and the potential risks and benefits not quantified. Wide-scale delivery could be achieved by drawing on expertise and approaches from the agricultural sector (i.e., fertilizer application can be considered nutritional supplementation of crops). Currently the approaches that would deliver an appropriate heterotrophic diet to coral *in situ* have not been developed. On a temporal scale, nutritional supplements would be applied during early and peak periods of environmental stress, and potentially even following the stress events to help coral recovery.

Risks

Ecosystem-level impacts include the effect of the addition of excess labile carbon, nitrogen, and phosphate into the reef environment on nutrient dynamics. Growth of species that more easily assimilate bioavailable carbon may be stimulated (e.g., macroalgae), allowing them to outcompete the corals that are already compromised. The additional carbon may also drive reef microbial processes that shift the flow of carbon through the food webs.

Within the coral itself, both nutritional extremes and change in the ratios of nutrients can disrupt the symbiosis between corals and their algal partners, making them more susceptible to bleaching (Wooldridge, 2009a, 2009b). Recent studies have linked declines in coral health to specific nutrient sources and ratios (D’Angelo and Wiedenmann, 2014; Wiedenmann et al., 2013) and hence if the nutritional balance of supplied food sources is poorly matched to coral physiological responses, the addition of these nutrient sources may lower coral resilience to environmental perturbations. Negative impacts are largely attributed to increased N:P ratios. While particulate food and moderate levels of ammonium and phosphate tend to benefit coral health and thermal tolerance (Béraud et al., 2013; Ezzat et al., 2016; Shantz and Burkepile, 2014), high nitrate negatively impacts coral health and reduces thermal tolerance unless accompanied by a higher level of phosphorus (D’Angelo and Wiedenmann, 2014; Rosset et al., 2017; Shantz and Burkepile, 2014; Wiedenmann et al., 2013). Consideration of the internal nutrient budgets of corals its influence on coral physiology is essential in prospective work that promotes nutritional supplementation of corals.

Limitations

Effectiveness is limited by poor understanding of coral diets and nutritional requirements and limited knowledge of species-specific responses to different nutritional supplements. There is a requirement for extensive development of technology and infrastructure to deliver heterotrophic nutrients to corals *in situ*. Nutrient encapsulation and formulations are well established in other industries (i.e., animal food industries) and can potentially be adapted to a novel challenge in the marine environment. Nevertheless, the suitability of the nutritional supplementation requires extensive evaluation with well-designed laboratory and aquarium-based experiments.

Infrastructure

A research and development phase would be needed to optimize coral diets. Subsequent costs and infrastructure would be moderate due to existing technologies in other sectors that could easily be adapted. Therefore, research targeted at developing improved coral diets is required and can draw on experience in other industries including human and veterinary health and agricultural systems for improving the efficacy of supplementation. This can include developing diets with broad benefits to coral health, not only through nutritional supply but also through improved delivery of microbial symbionts (i.e., probiotics cocktails containing both algal and prokaryote communities) and other beneficial augmentation (e.g., antioxidants). The infrastructure needed to deliver heterotrophic coral diets at the scale of reefs at this stage is unknown without extensive feasibility testing and development. At the aquarium scale, these systems and approaches are already implemented.

4

Coral Population and Community Interventions

In contrast to most genetic and physiological interventions, which target individual corals with the ultimate purpose of changing entire coral populations, this chapter discusses interventions that seek to directly alter entire populations or communities of coral. This chapter groups together three interventions: assisted gene flow, assisted migration, and introduction to new areas. In practice, these three interventions can be seen as tiered scales of managed relocation in support of varying goals. Managed relocation is the introduction of a particular genotype or an entire species to areas outside the historical bounds for a given genotype or species. Managed relocation is a component of the broader concept of translocation—the movement of individuals in space—which also includes reintroduction following habitat restoration in historically-occupied locations (Armstrong and Seddon, 2007; Griffith et al., 1989). Assisted gene flow supports the expansion of resilient genotypes within a coral's current range. Assisted migration supports movement of corals to areas just outside their range, which they may be better suited to as climate change causes preferred habitat to shift to higher latitudes. Introduction to new areas involves the introduction of non-native coral that may be more tolerant to stressed conditions, in order to maintain the presence of the coral reef.

Large-scale relocation of coral has not been trialed, but lessons can be drawn from other taxa or from corals that have been moved to, or outplanted from, coral nurseries, reciprocal transplant experiments, reef restoration efforts, accidental introductions, and natural range expansions. These lessons provide a significant knowledge base for evaluating the approach in detail, including potential benefits, feasibility, risks, and limitations.

MANAGING CORAL PREDATORS, COMPETITORS, AND FACILITATORS

Corals are not the only potential targets when managing a coral reef community, and the health and diversity of other members of the community have a direct influence on the health and resilience of the coral species. The diversity of reef communities derives from the hundreds of species of fish, invertebrates, algae, protists, and microbes that typically live among corals. In almost all cases, these species also play a huge role in the value of reefs to humans—through recreation, fishing, algal farming, and other services. As a result, managing coral communities is more than just managing corals: though corals play a fundamental role, management of other species is also important.

Maintaining ecological processes and community dynamics has been identified as important factor in facilitating coral restoration success (Ladd et al., 2018; Shaver et al., 2018). This includes managing herbivory by fish and urchins to minimize algal competition, coral predation by fish and invertebrates, and nutrient cycling by fish. Non-coral individuals and species may be targets of managed relocation in combination with coral. While the focus of this chapter is on the coral-specific goals, the committee does discuss some considerations of moving reef-associated exosymbionts and herbivores in order to increase the likelihood of coral relocation success. Additionally, some reef-associated species are targets of existing management practices described in Chapter 1, such as management of overfishing and invasive species.

MANAGED RELOCATION

What It Is

Managed relocation is the movement of species, populations, genotypes, or phenotypes from a source area to locations outside of their historical distribution, sometimes with different environmental parameters (Richardson et al., 2009; Schwartz et al., 2012). Managed relocation typically focuses on moving individuals to promote adaptive response to climate change (Schwartz et al., 2012), by moving populations or species to locations with future climatic conditions analogous to what they historically experienced.

Managed relocation to promote adaptive responses to climate change has already occurred in a variety of taxa, and more are being planned. Examples of species where relocations have occurred include an endangered conifer (*Torreya taxifolia*) in the southwestern United States (Barlow, 2010) and two butterfly species in the United Kingdom (Willis et al., 2009), and discussions are under way for relocations in the forestry industry (McKenney et al., 2009) and in commercial fisheries (e.g., lobsters; Green et al., 2010). There are no examples of large-scale managed relocation of corals, but assessments of its potential may be gleaned from corals that have been moved to or outplanted from coral nurseries, reciprocal transplant experiments, reef restoration efforts, accidental introductions, and natural range expansions. With concerns about coral reef persistence under future climate change and multiple anthropogenic stressors, managed relocation of corals has been considered albeit with caution (Hoegh-Guldberg et al., 2008).

Managed relocation is categorized into three types (depicted in Figure 4.1):

Assisted gene flow is the movement of genotypes within a population’s range (Aitken and Whitlock, 2003). Assisted gene flow typically focuses on the relocation of individuals with genotypes that confer higher stress tolerance, which requires that populations exhibit genetically-based variation in stress tolerance across locations with different historical levels of stress exposure. For example, some Pacific populations of corals live in highly variable or warm water microhabitats (Oliver and Palumbi, 2011). These corals can provide nursery stocks with high heat tolerance (Morikawa and Palumbi, in press).

Assisted migration (also called assisted colonization) is the movement of individuals beyond a species’ range boundaries (Schwartz et al., 2012). Climate change can cause locations just outside of a species’ range to have environmental conditions analogous to historic conditions within a species’ range, such that range shifts to these locations can contribute to species’ persistence under climate change (Davis and Shaw, 2001). Corals at some locations, including corals in Japan, Florida, and Australia (Baird et al., 2012; Greenstein and Pandolfi, 2008; Precht and Aronson, 2004; Yamano et al., 2011), already exhibit natural and detectable poleward range shifts in response to climate change (Parmesan and Yohe, 2003). Therefore, the typical focus is movement just beyond a species' range in the poleward, or otherwise cooler or lower-stress, direction.

Introduction to new areas is the movement of highly stress-tolerant individuals between regions, such as, in the extreme, between ocean basins (Coles and Riegl, 2013; Sheppard, 2003). For example, corals in the Red Sea can maintain photosynthetic performance up to 32°C, nearly 6 °C above average summer maximum (26.1° C) but within natural fluctuations for shallow regions (Fine et al., 2013). Corals from the Gulf of Oman can exist over a wide range of temperatures from 11.4° C to 36°C (Coles, 1997).

Because of the overlap in goals, methodologies for How to Do It, limitations, and risks between these three types of relocations, they are discussed together in this chapter, with any differences highlighted.

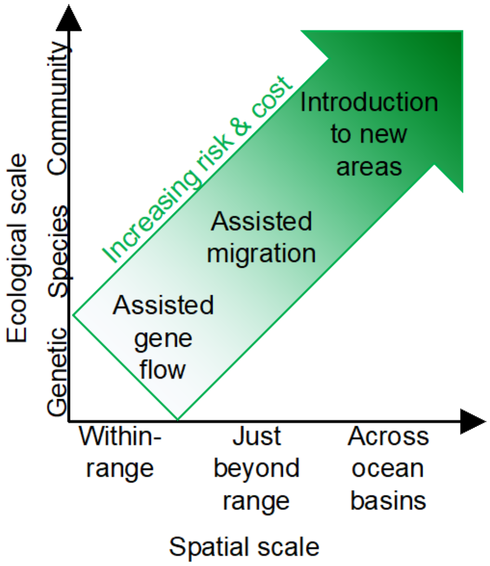

FIGURE 4.1 Typical ecological scale and spatial scale of the different relocation types, where risks and costs both increase with scale.

Benefit and Goals

Managed relocation often focuses on one or both of two distinct ultimate goals. First, the most-commonly invoked goal of managed relocation across taxa is to reduce the likelihood of extinction for a species, population, or genotype vulnerable to climate change (Hewitt et al., 2011; Schwartz et al., 2012). This could involve moving corals that are vulnerable to extinction to locations where future predicted oceanographic conditions are expected to be more suitable. Second, managed relocation might promote the maintenance of the ecosystem state in a particular location, such as coral-dominated reefs and the associated species assemblage and ecosystem services (Hewitt et al., 2011; Schwartz et al., 2012). This is particularly relevant to foundational taxa such as corals, which provide the structure of reef communities (Wild et al., 2011). This could involve importing individuals from populations with temperature tolerance (Bay and Palumbi, 2014; Loya et al., 2001), disease resistance (Vollmer and Kline, 2008), and tolerance to sedimentation or acidification (Fabricius, 2005). The overarching goal of promoting the maintenance of a particular ecosystem state might take on many forms, from having corals as the primary benthic taxa regardless of species composition, to maintaining a complex topography that supports diverse fish and invertebrate communities (Graham et al., 2006; Gratwicke and Speight, 2005; Wilson et al., 2006) and associated ecosystem functions such as reducing wave stress (Storlazzi et al., 2017), maintaining tourism, and providing sand production. Therefore, managed relocation to promote an ecosystem state might involve the relocation of multiple species in a coral community assemblage.

Management actions may include some combination of these goals, focused on both preserving specific species and maintaining place-based reefs, but their clear definition at the outset will clarify potential costs, benefits, and risks. In addition to the two overarching goals that can apply to all relocations, proximate goals vary with relocation type.

For **assisted gene flow**, a key proximate goal is to enhance the spread of stress-tolerant alleles and their transmission into the next generation. An additional potential goal is to enhance genetic diversity within target populations to overcome low fertilization success at low colony densities (Allee effects) and at low intraspecific genetic diversity due to obligate outcrossing in some species (including the major reef-building corals of the Caribbean; Miller et al., 2018), thereby enhancing reproductive success during spawning events (Baums, 2008; Miller et al., 2018). These goals align when the addition of new, stress-tolerant, genotypes to an area also increases genetic variation generally and when sexual reproduction further increases genetic variation in stress tolerance. There is overlap in goals of assisted gene flow and managed breeding (described in Chpater 2), where assisted gene flow is specifically focused on the transport between locations as an approach to achieve these goals.

Natural levels of gene flow vary widely among coral species (Ayre and Hughes, 2000) but can, in some cases, be low over scales of hundreds to thousands of kilometers (Sheets et al., 2018; Torda et al., 2013; Wood et al., 2014). Assisted gene flow can promote genetic connectivity between reefs along gradients of thermal stress (Baskett et al., 2010; Bay et al., 2017; Matz et al., 2018). A genomic model by Bay et al. (2017) showed that incorporation of 10 adult breeding colonies of heat-tolerant coral from Samoa could enhance evolution of heat tolerance in nominally cool-adapted populations in the Cook Islands, but that natural dispersal between these localities, about 1,000 km apart, was far smaller than that. Therefore, assisted gene flow can be relevant if frequencies of known adaptive alleles are low and if diversity or abundance of native colonies is low.

For **assisted migration**, a key proximate goal is to promote range shifts along latitudinal or analogous gradients to track changes in climate. Poleward relocations are frequently proposed in the literature (Baird and Thomson, 2018; Hoegh-Guldberg et al., 2008; Riegl, 2003; Riegl and Piller, 2003; Tuckett et al., 2017). Surveys of genetic differentiation in corals suggest that natural migration over 500-1,000 km is rare (usually less than one successful migrant per generation). As an example, only four species of the most speciose genus of corals, *Acropora,* is established in Hawaii (Grigg et al., 1981; Walsh et al., 2014). Increased clonality of edge populations (Baums et al., 2014; Foster et al., 2013; Miller et al., 2018) might further limit natural range expansions for obligate outcrossers.

Migration along north-south coastlines might occur more rapidly by a stepping-stone mechanism such as along the west coast of Australia or along the Ryukyu Islands towards the main islands of Japan. Range shifts are typically more rapid in the oceans than on land despite slower overall climate velocity (the movement of zones of suitable climate) in the ocean, which might be due to lower heterogeneity in climate velocity among locations (Burrows et al., 2011) as well as greater dispersal potential. While geological evidence suggests that subtropical reefs have acted as important refugia in the past for tropical corals (Greenstein and Pandolfi, 2011; Halfar et al., 2005; Kiessling, 2009), some have questioned the likelihood that high-latitude ecosystems would actually be able to support viable tropical populations (Beger et al., 2014), in part because they are (at present) marginal environments for corals, for reasons such as reduced aragonite saturation (Guinotte et al., 2003), higher temperature variability, and limited winter light availability (Muir et al., 2015).

For **introduction to new areas**, a key proximate goal is to enhance stress tolerance of the local reef assemblage by adding species at the recipient location. While this proximate goal is focused on maintaining reef-dominated states, introduction to new areas can contribute to the goal of preserving a threatened species if the potential source locations are also threatened by climate warming and largely isolated from other populations (as is the case for the Persian Gulf; Coles and Riegl, 2013).

How to Do It

Engaging in managed relocation is a multifaceted process with a variety of approaches to determining (1) whether to translocate, (2) how and at what stage to move individuals, (3) which species and individuals to move, (4) what is the best source or target location, and (5) when, how often, and for how long to translocate (Figure 4.2; Pérez et al., 2012; Schwartz and Martin, 2013). Tools including vulnerability assessment, risk-benefit analysis, and feasibility assessment have been developed to guide the relocation process, with existing decision analysis tools for managed relocation particularly focused on (1) and (3) (Figure 4.2; Hoegh-Guldberg et al., 2008; Pérez et al., 2012; Schwartz and Martin, 2013; Weeks et al., 2011).

The decision to translocate

Managed relocation is relevant when limited dispersal, slow population growth, small populations, or fragmented habitat distribution impede natural movement responses to climate change or other such stressors (Hewitt et al., 2011). As sessile, benthic organisms with only limited movement potential associated with growth and fragmentation, any coral dispersal beyond a few meters can normally only occur through gametes and larvae. Specifically, while tissue covered fragments and sloughed tissue may travel short distances from the parent colony (Sammarco, 1982), coral larvae typically disperse distances of hundreds of meters to several kilometers, and on occasion, can travel over hundreds of kilometers (Graham et al., 2008). Natural dispersal may also be limited by arrival in insufficient numbers or diversity to establish. If the populations are small, establishment might fail due to processes such as demographic stochasticity (random variation in individual survival, growth, and reproduction, where extreme outcomes such as few survivors are more likely in small populations), environmental stochasticity (random variation in environmental conditions, including extreme events such as hurricane disturbances), demographic Allee effects (threshold population sizes necessary for population growth), genetic drift (random loss of genetic diversity at low population sizes), and inbreeding (exposure of deleterious recessive alleles in small populations; Gilpin and Soule, 1986; Lande, 1998). An additional limitation to successful dispersal for some corals arises due to obligate outcrossing, where low genetic diversity can lead to recruitment failure (Baums, 2008; Miller et al., 2018), essentially a diversity-dependent Allee effect. Obligate outcrossers comprise the major reef-building corals of the Caribbean (Miller et al., 2018), where low diversity might help explain the decline in observed recruitment (Miller et al., 2018; Williams et al., 2008).

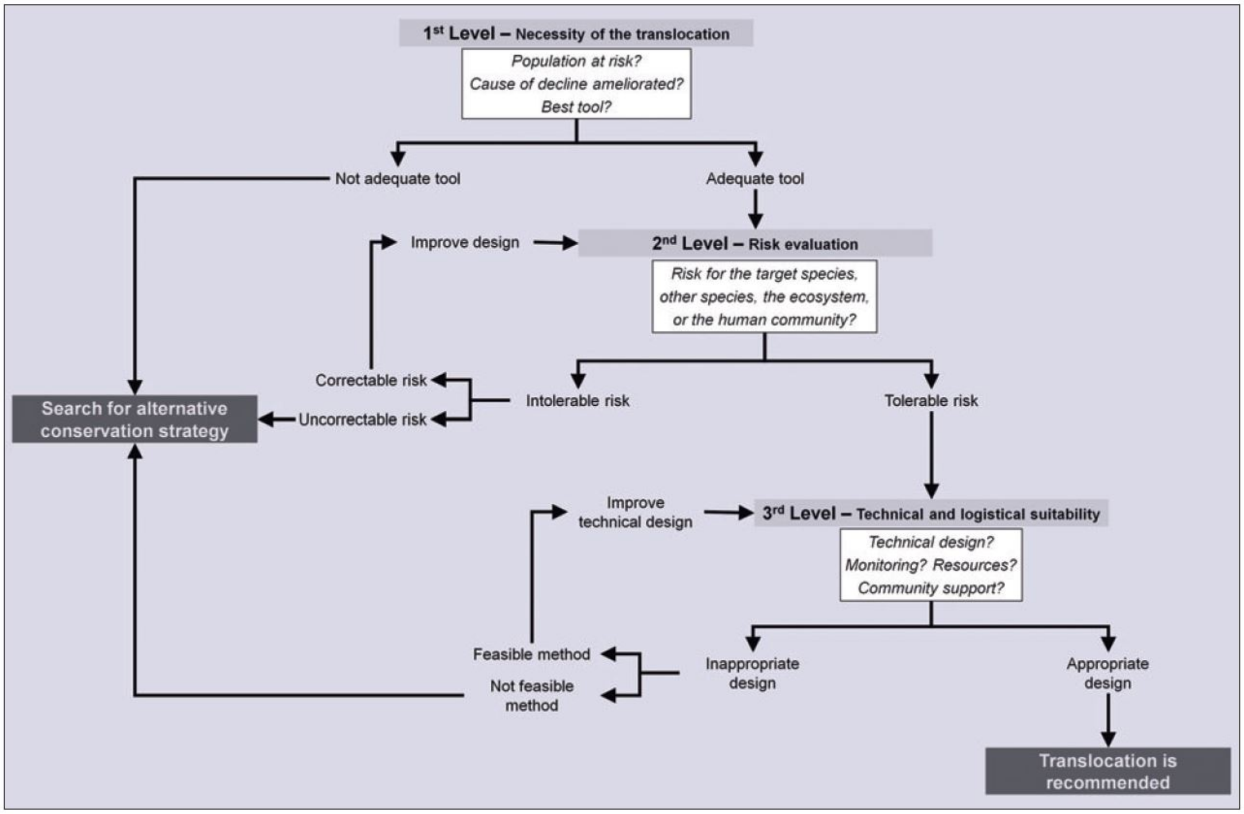

Figure 4.2. Example managed relocation decision-making protocol that accounts for relevancy, risks, feasibility, and alternatives. For the first-level assessment of the necessity of relocation, see the “How to Do It: The decision to relocate” section. For the second-level assessment of risk evaluation, see the “Risks” section. For the third-level assessment of technical and logistic suitability, see both the “How to Do It” and the “Feasible now” sections. SOURCE: Pérez et al., 2012.

How and at what stage to move

The typical coral relocation process involves collecting colony fragments, growing fragments in nursery settings, and replanting nursery clones in different reef areas. The options are broad, and moving corals could occur at different life stages (e.g., larvae, juveniles, or adults), with or without use of an intermediate facility. Bringing larvae, colonies, or fragments collected in the field into laboratory or nursery facilities can allow for acclimation to different conditions, including those expected at the recipient site, as well as a quarantine period to reduce the risk of spreading diseases and invasive species (Edwards, 2010). Coral transplantation has been a feature of basic coral biological research for decades (e.g., Edwards and Clark, 1999; Harriott and Fisk, 1988; Yap, 1994; Yap et al., 1992) especially in the field of morphological plasticity (e.g., Foster, 1979). Transplant survival can be low in some settings (Edwards and Clark, 1999) but can be enhanced through careful handling, feeding, or other protocols (Barton et al., 2017; Lirman and Schopmeyer, 2016; Toh et al., 2014).

The first step in any relocation is to remove individuals from the source location. It is important to minimize damage to the source population, particularly if the goal is to move a species already under threat. The least damaging extraction method may be at odds with the method that would maximize relocation success in the new location. For example, the life stage that is probably least damaging to extract and easiest to move is coral larvae, but larvae may also be the least likely to succeed in the new location compared to adults (Edwards et al., 2015). An intermediate approach is the most common: removing small fragments of source colonies and growing corals in nurseries prior to outplant (Young et al., 2012). This can reduce the impact on source populations and increase outplant success. An additional approach to mitigating the impact on source populations is the use of “corals of opportunity,” such as those that would be damaged during a dredging project if they were not moved, or fragments resulting from a ship grounding. Collecting coral fragments that have been damaged by storms or ships also has low impact on source populations but generally has low success (Ferse, 2010; Garrison and Ward, 2012).

If the goal is to use managed relocation to re-establish a reef ecosystem in a particular place regardless of coral species composition, implementation becomes more challenging. The continuum of possible goals is broad, ranging from creating a simple three-dimensonal coral structure to support fish communities to restoring ecological complexity and ecosystem services (Rinkevich, 2014). The coral reef restoration community can offer insights into how such a task might be approached (Johnson et al., 2011; Ladd et al., 2018; Lirman and Schopmeyer, 2016; Rinkevich, 1995; Young et al., 2012), but the underlying science for how to take this approach is still in its infancy, particularly in regards to large-scale collection and nursery culturing of non-native species for transplantation from outside of the species historical range.

Following removal from the source location, the subsequent steps for relocation are cultivation of coral propagules and reattachment, as described in Box 2.1. Long-term relocation success requires the survival, reproduction, and recruitment of transplanted corals (Richmond et al., 2018), which might rely on reducing local stressors or additional restoration efforts (e.g., algal removal, reintroduction of herbivores) as part of the relocation program design. Especially in cases where current reef communities are degraded, relocation is very unlikely to restore populations unless the underlying cause of degradation (e.g., sedimentation, loss of herbivores) is reversed. Relocations to advance the gene flow of adaptive alleles into a healthy population with fewer local stressors, lower algal cover, and more abundant and diverse herbivore communities may be more successful. Best practices for managed relocation, from propagation and outplanting techniques to identification of appropriate abiotic and biotic conditions in outplanted locations, mirror those of coral restoration, reviewed in Ladd et al (2018), Lirman and Schopmeyer (2016), Meesters et al. (2015), and Young et al (2012).

One potential consideration in reattachment is the density and composition of relocated corals. In coral restoration projects, densities of outplanted corals vary widely (0.1-25 corals/m^2), with little data on how density affects restoration success despite its expected importance (Ladd et al., 2018). High density of a focal coral species can overcome Allee effects (e.g., increase spawning success), diffuse corallivore predation, and reduce competition from other benthic competitiors (e.g., sponges, algae), but low density can decrease disease spread and intraspecific competition for space (Ladd et al., 2018).

How to identify which species and individuals to move

The focal species, or assemblage of species, for relocation depends on the management goal. If the goal is to prevent extinction of climate-vulnerable species, then the focus will be on stress-vulnerable species as indicated by characteristics such as limited dispersal, rarity, low fecundity, long generation times, and susceptibility to thermal stress (Chauvenet et al., 2013; Hewitt et al., 2011; Loss et al., 2011). If the goal is to protect coral-dominated reefs, then the focus might be on stress-tolerant individuals or species as those most likely to persist through future stress (Côté and Darling, 2010). However, a focus on a diverse assemblage might also be the target for a goal of protecting coral-dominated reefs given the role of diversity in adaptive capacity, ecological resilience, and ecosystem function and service provisioning as highlighted in Chapter 1 (Levin and Lubchenco, 2008). One of the strongest results from careful bookkeeping of success of coral fragments is that different genotypes can express different survival, growth, and stress-resistant phenotypes (Morikawa and Palumbi, in press). These variants might be used in outplanting into different locations, might show tradeoffs between different fitness traits (such as growth versus heat resistance), and might provide a buffer against genetic erosion of nursery stocks.

Managed selection (Chapter 2) is an approach for identifying coral with stress-tolerant genotypes. For **assisted gene flow**, identification of stress-tolerant genotypes might use emerging molecular tools such as genomics, proteomics, transcriptomics, and metabolomics, which provide insight into the cause-and-effect relationships between stressor exposure and response at the levels from cells to ecosystems (Downs et al., 2005, 2012). While promising, these tools are likely to be species-specific and, because they are typically identified under short-term heat-stress experiments, they may not be indicative of long-term heat tolerance (Louis et al., 2017). Instead, direct physiological testing of reef corals collected from native environments has been shown to be effective, and provides high predictive ability in comparisons of coral clones in nurseries (Morikawa and Palumbi, in press). For **assisted migration**, coral morphology can also be an indicator of major coral taxa that generally show high stress tolerance or susceptibility. For example, massive corals, with perforate skeletons with tissues sequestered deeper in the skeleton, are generally more resistant to particular stressors including bleaching, than other, branching, nonperforate types (Hoegh-Guldberg and Salvat, 1995; Loya et al., 2001; van Woesik et al., 2011).

For **introduction to new areas**, in addition to stress-tolerance, a focus may be on growth forms that provide fish habitat, reef structure, and associated coastal protection. A diversity of coral morphologies typically predicts fish diversity—coral height predicts fish abundance, and larger-bodied fish disproportionately use tabular corals as habitat—where fish diversity, abundance, and body size contribute to different aspects of ecosystem function and services (Gratwicke and Speight, 2005; Kerry and Bellwood, 2012).

Regarding species composition, a consideration for relocation success is the potential for interspecific competition between corals. Arborescent (tree-like) and table corals can grow quickly above massive and encrusting species, while massive and encrusting forms can outcompete some branching species through mechanisms such as chemical defense, sweeper tentacles, and mesenterial filaments that digest the tissues of nearby neighbors (Chadwick and Morrow, 2011; Connell et al., 2004; Lang and Chornesky, 1990; Rinkevich and Loya, 1985). Despite competition, diversity might increase outplant success if it enhances ecosystem function through a diversity of functional types (e.g., massive corals buffering against currents and wave action while foliose and arborescent forms provide reef rugosity and herbivore habitat), reduces competition with other benthic species, or reduces corallivory through a mix of palatable and nonpalatable species (Ladd et al., 2018).

How to identify source and target locations

The target location depends on the relocation type and goal. For example, a goal of building reef structure at vulnerable locations will target high-stress locations, while a goal of promoting intact reef structure where future persistence is most likely will focus on lower-stress locations. Likewise, goals of promoting higher frequencies of adaptive alleles in otherwise established populations will tend to target populations predicted to experience high stress in the future. A management focus on low-stress locations can more effectively achieve a goal of promoting coral cover in a higher-disturbance future, as can high-stress locations in a lower-disturbance future (Game et al., 2008), where the magnitude of disturbance might be more relevant than the frequency in defining “high disturbance” (Fabina et al., 2015). However, in some ocean basins, such as the Caribbean, low-stress locations may be rare. For an example of identification of low-stress locations as a target, Beyer et al. (2018) identify reef locations globally that may be prime locations for restoration in the absence of local disturbances, based on both connectivity and a number of climate variables.

Using a combination of meteorological, oceanographic, and *in situ* coral reef monitoring data, it is possible to identify specific areas that have been or are likely to be affected by temperature-induced heat stress (Hughes et al., 2017a). Such areas can be source locations from which corals might be removed for transplantation to areas less likely to be affected (McClanahan et al., 2012). Such heat-tolerant populations might be large in extent, for example if they exist across broad latitudinal gradients such as along the Great Barrier Reef (Berkelmans and van Oppen, 2006; Dixon et al., 2015; Howells et al., 2013), but they can also be small in extent when the environmental mosaic is over short distances such as fore reef versus patch reef or reef crest areas (Oliver and Palumbi, 2011; Morikawa and Palumbi, in press). A global search for generalized areas likely to house heat-resistant coral colonies has yet to be done, but might include areas under heat stress during daytime low tides (back reefs, patch reefs; Oliver and Palumbi, 2011), equatorial reefs (Jokiel and Coates, 1980), or corals near powerplants (Keshavmurthy et al., 2012), or regions of high-frequency temperature variability (Safaie et al 2018). At the local level, monitoring and mapping of coral reefs can also identify those areas most affected by conditions contributing to losses. For environmental conditions besides the focal stressor, analogous conditions between source and target locations (e.g., in depth, illumination, turbidity, and salinity) might increase relocation success as corals from a source area with similar conditions to the explant site are more likely to survive, grow, and reproduce.

A further consideration is connectivity between sites. Promoting range shifts through assisted gene flow or assisted migration relies on connectivity between reefs and therefore might focus on target locations that confer connectivity to downstream reefs (e.g., across environmental gradients). Alternately, promoting population or reef persistence in vulnerable locations may lead to a focus on isolated locations where natural or anthropogenic barriers impede dispersal. Corals do show variability in their degree of isolation across locations (Baums et al., 2005), where identification of isolated locations relies on genetic data, oceanographic models of larval dispersal, or a combination (Foster et al., 2012). Considered alone, genetic isolation might indicate limits to connectivity, or it might indicate post-settlement barriers to establishment. In the latter case, relocation is either not necessary (if thermal regime historically served as a post-settlement barrier) or will be unlikely to succeed (if other environmental factors serve as the post-settlement barrier). Therefore, a combination of oceanographic-based connectivity and genetic data holds the greatest promise to identify locations with physical barriers to dispersal.

One tool for identifying source and target locations in managed relocation is to use species distribution modeling (SDM) to match historic (source) and future (target) climatic conditions between locations (Kreyling et al., 2011). Either combining SDMs with the analyses of connectivity described above or extending the basic SDM framework to directly incorporate dispersal (reviewed in Elith and Leathwick, 2009) would be necessary to identify relevant locations not already connected by natural dispersal. SDMs have been used to identify suitable climate envelopes for managed relocation under future climate change for trees, plants, and reptiles (Fordham et al., 2012; Gray et al., 2011; Regan et al., 2012). Freeman et al. (2013) used a Maxent global bioclimate modeling approach to show that shallow tropical corals within the Indian Ocean currently experience physiochemical conditions most similar to future worldwide conditions under climate change. These authors suggest that this region might be a good source of corals for future managed relocation efforts based on climate matching.

Much like source populations from marginal habitats, identification of recipient locations might capitalize on corals of opportunity. Specifically, new restoration projects taking place at highly degraded sites, which are increasing in the Caribbean (Young et al., 2012), might present unique opportunities to engage in all types of managed relocation by focusing on sources from either more stress-tolerant populations or with a diversity of stress tolerances or stress histories (Broadhurst et al., 2008; Rice and Emery, 2003; Sgrò et al., 2011). Implementing relocation through existing restoration projects can reduce costs and the risks to existing degraded recipient communities described below. However, success would likely be lower than if relocation targeted less degraded sites and could require reduction or elimination of stressors that originally led to coral reef degradation. If the goal were to choose locations with the highest likelihood of relocation success, coral restoration practitioners identify herbivore populations, substrate availability (e.g., low cover of coral competitors such as algae and sponges), and coral cover (as an indicator of habitat quality and to diffuse corallivory) as key factors for selecting target restoration sites (although few studies document the effect of these factors on restoration success; Ladd et al., 2018).

How to identify when to translocate

The decisions for the timing of a relocation project might take a proactive approach of translocating in anticipation of future change or a reactive approach of translocating in response to declines. The proactive approach can rely on SDMs of environmental drivers of coral distributions under present conditions and projected suitable habitat under future conditions (Chauvenet, 2013; Gallagher et al., 2011; Gray et al., 2011). Combining SDMs with population dynamic models will provide added information on anticipated persistence under different management approaches (Bonebrake et al., 2014; Chauvenet, 2013; Fordham et al., 2012; Regan et al., 2012). The reactive approach relies on monitoring of coral cover through time to detect declines, where temperature recorders (currently available) can guide identification of at-risk locations to monitor.

Current Feasibility

On a technical level, many aspects of collection, transportation, and outplanting are feasible. However, a much greater feasibility challenge to managed relocation is in the information necessary to make the multifaceted decision of whether, what, how many, when, and where to translocate as well as to assess the risks described below.

Moving individuals at different stages

The practice of "coral gardening" is increasing in the Caribbean and elsewhere (Young et al., 2012), applied to a variety of species (Rinkevich, 2014), with well-developed propagation techniques (Barton et al., 2017). While outplanting is occurring at ecologically-relevant scales (Lirman and Schopmeyer, 2016), cost can remain a barrier to scaling up in regional restoration projects (Young et al., 2012). In addition, while the drivers of nursery and outplanting success are well-studied, how the overall project design and ecological processes affect project success is less well-known (Ladd et al., 2018). The cost and complexity will inevitably increase with the project scale in terms of distance transport, number of colonies moved, and number of repeated transports, such that we expect the feasibility of assisted gene flow and assisted migration to be significantly less than that of introduction to new areas (as depicted in Figure 4.1).

While technically feasible, relocation practices are far from perfected. Previous efforts have shown that direct translocation often results in mortality of transplants, generally in the range of 30% (Piniak and Brown, 2008). Losses may occur due to stress associated with handling and increase with both distance and time from collection to transplantation (Naughton and Jokiel, 2001). Problems also result from environmental differences between the donor and receiving sites. Site characteristics such as wave exposure, turbidity, water quality, and substrate stability affect the survival of transplants (Jokiel and Naughton, 2001). Corals taken from deeper depths placed into shallower waters may bleach due to increases in temperatures and light intensities (Lenihan et al., 2008).

While moving and propagating fragments is feasible now, the techniques for fertilizing and moving eggs in captivity are still under development. This approach requires freezing gametes (see Coral Cryopreservation in Chapter 3) or in-tank spawning (see Gamete and Larval Capture and Seeding in Chapter 3). Recent advances (e.g., SECORE and CORALZOO projects) include successful fertilization and settlement of larvae that are now part of active restoration projects, with ongoing research into survival likelihood and its drivers (Lirman and Schopmeyer, 2016; Meesters et al., 2015).

Identifying whether and what species and individuals to move

The feasibility of identifying the level of stress-tolerance or stress-susceptibility depends on the approach (see comparison of proxy-based and direct approaches in Morikawa and Palumbi, in press). Using environmental proxies will require information on past environmental conditions, which is attainable at coarse spatial scales but potentially more difficult to attain at the finer spatial scales relevant to local acclimation and adaptation. Using biotic characteristics or direct measurements of stress tolerance might require more information gathering. Therefore, environmental proxies might be more feasible to use but will also confer greater uncertainty as they provide indirect rather than direct measures of expected stress tolerance.

For the goal of preventing extinction of climate-vulnerable species, identification of such species can rely on direct or indirect indicators of vulnerability. Direct indicators such as mortality under past stress, population declines, range contractions, and range shifts slower than other species in the community require ongoing monitoring of coral systems, which is feasible but costly. Where long-term monitoring data on population sizes are not present, population trends can be inferred from genetic markers (e.g., A. Chan et al., 2018). In the absence of such direct indicators, indirect indicators of stress susceptibility such as coral morphology are readily available but confer greater uncertainty. Identification of dispersal-limited species, an indicator of both climate vulnerability and the relevance of managed relocation, through genetic data and/or oceanographic models of larval dispersal is feasible but requires investment. For identifying species with low thermal tolerance, dispersal limitation, or other such indicators of vulnerability, the Coral Traits Database (coraltraits.org; Madin et al., 2016) includes scoring of relevant traits such as bleaching susceptibility, fecundity, generation time, spawning date, and egg size.

Beyond the level of stress tolerance or vulnerability, a challenge to identifying a target species is the difficulty in distinguishing coral species in the field due to a high degree of plasticity and polymorphism as well as a high degree of hybridization in corals (Stat et al., 2012). High phenotypic plasticity, including in skeletal morphology, has long been recognized as a challenge to coral taxonomy (Bernard, 1902; Tisthammer and Richmond, 2018). Genetic analyses in the laboratory can differentiate coral species that are visibly similar and reveal cryptic species within existing species delineations (e.g., Knowlton et al., 1992; Ladner and Palumbi, 2012; Warner et al., 2015), hybridization between delineated species (e.g., Forsman et al., 2017; Szmant et al., 1997), and that delineated species are themselves hybrids of other species (e.g., Vollmer and Palumbi, 2002). Cryptic species and hybridization lead to conflicting conclusions regarding species delineation for well-studied genuses (e.g., *Acropora*, *Orbicella* [formerly *Montastraea*], *Pocillopora*), with ongoing debate over the appropriate molecular markers to distinguish species (Stat et al., 2012). This is especially true when closely related species share many polymorphisms (e.g., Ladner and Palumbi, 2012), resulting in good species resolution only when large numbers of polymorphic markers are used. New approaches with genome-wide data tend to show clearer distinctions among even closely related coral species (e.g., Rose et al, 2018), but are costly and slow. In some cases, identification of cryptic species complexes led eventually to morphological methods that could identify them (e.g., *Orbicella*, Knowlton et al., 1992). In other cases, some morphologically identical colonies are in different species but some morphologically divergent colonies are not (e.g., *Pocillopora damicornis*, Pinzón and LaJeunesse, 2010; Torda et al., 2013)

Given stress-tolerant target individuals or species, whether the stress tolerance observed in the source location will be analogous to that in the target location will depend on three key unknowns. First, while both genetics and plasticity contribute to stress tolerance (Bay and Palumbi, 2014, 2015; Liew et al., 2018b), their relative roles are unresolved for most corals (with exceptions; Palumbi et al., 2014). Second, while stress tolerances such as thermal tolerance and disease resistance are holobiont properties that arise from a combination of the coral host, symbiotic zooxanthellae, and microbiome, their relative contributions are typically unresolved. Third, how much transplanted corals adopt local symbiotic zooxanthellae and microbiomes, as compared to maintaining source-location symbionts, is uncertain (in Smith et al., 2009, aquaria corals typically maintain native symbionts, but whether this carries over to outplanted corals is unknown) and will inevitably depend on the managed relocation approach, stage at relocation, and coral life history.

Identifying where and when to move

Information necessary to parameterize the species distribution and demographic models that can inform decisions of when and where to move is attainable but might require significant investment. This includes existing species distributions and local-scale environmental conditions such as temperature for SDMs (Elith and Leathwick, 2009), and size- and environment-dependent survival, reproduction, and growth for demographic models (Edmunds et al., 2014). A challenge to applying SDMs to managed relocation is uncertainty and variability in their ability to accurately predict future suitable habitat (Dobrowski et al., 2011). In addition, most predictive models do not mechanistically incorporate the capacity for species to acclimatize or adapt to their environments (Sgrò et al., 2010), although recent efforts have attempted to do so for corals at the global scale (Logan et al., 2014) and at regional scales (e.g., Baskett et al., 2009; Bay et al., 2017; Matz et al. 2018).

Managed relocation decisions will further rely on additional information regarding population and community characteristics. For example, the decision of how many to relocate will rely on knowledge of threshold population sizes for expected increase (as it might depend on Allee effects or demographic stochasticity; Gilpin and Soule, 1986) or coral densities for expected reef persistence (as it might rely on interactions with macroalgae; Mumby et al., 2007). Quantitatively precise information on these thresholds is unlikely to be available, which does not impede project implementation but does introduce uncertainty. In addition, the decision for where to translocate might depend on the degree of site isolation as described above, where attaining the relevant genetic and/or oceanographic data on connectivity is feasible (and exists for some species; e.g., *Acropera palmata* in Baums et al., 2005 and *Orbicella annularis* in Foster et al., 2012) but may require investment.

Potential Scale

The distance between a source population and a target location ranges from within a population's range to across ocean basins, depending on the relocation type (Figure 4.1). Typically the distinction between relocation types is based on the spatial scale of a species range, but many coral species' boundaries span entire (and sometimes multiple) ocean basins (e.g., many Caribbean species are basin-wide). Therefore, the appropriate boundaries depend on the scale of genetic differentiation.

The practical scale of implementation at a new location is on the scale of meters to kilometers, similar to the scale of coral restoration efforts.

The temporal scale in terms of both duration and frequency can range from a one-off relocation to a sustained program over several years, depending on the management approach, goals, risk perception, resources, and success. More frequent and longer relocations will buffer against the risk of a catastrophic event negating the project and increase success likelihood through repeated trials, but it will also increase the risk relocation described below. In addition, the duration of a relocation program will depend on the trajectory of continued greenhouse emissions or other such stressor, with the potential for "conservation reliance" (i.e., requiring continued management intervention; Scott et al., 2010) unless relocations or other management actions can establish reefs along connectivity gradients that eventually allow natural dispersal to occur.

Scaling up to multiple species might include considerations of whether to translocate additional functional groups that are important to the maintenance of coral-dominated systems. Two such functional groups are coral exosymbionts (e.g., crustaceans that clean and guard corals; McKeon et al., 2012; Stier et al., 2012) and herbivorous invertebrates and fish. Exosymbiont and herbivore managed relocation is a consideration if factors that limit natural coral dispersal to the recipient location also limit those of the target functional group. For assisted migration or introduction to new areas, moving exosymbionts or herbivores might be relevant if the communities of these functional groups in the recipient location cannot associate with the translocated coral(s) due to a high degree of host specialization. The value of active relocation is also dependent on the stress tolerance (for assisted gene flow) and natural dispersal capabilities of these organisms. Exosymbionts do show host specificity (Stella et al., 2010) and local-scale variation (Rouzé et al., 2017), but information on the drivers of their distribution is limited. Expected scales of herbivorous fish dispersal are on the order of 10-100 km (Cowen et al., 2006), and the impacts of climate change on their growth, survival, and reproduction vary from negative to positive, with the impact of habitat loss from coral bleaching likely outweighing any direct thermal stress (Munday et al., 2008). Herbivorous fish can also be impacted by due to thermal stress independent of coral mortality, as observed in the most recent bleaching event on the Great Barrier Reef. (Stuart-Smith et al., 2018). Therefore, while a potential consideration, whether relocation of exosymbionts and herbivores is necessary for coral reef ecosystem response to climate change is uncertain.

Risk

A key risk for all managed relocation types is the introduction of non-native pathogens, parasites, algae, microbes, commensal invertebrates, and corallivores (e.g., gastropods) that might overwhelm local controls on their abundance. Such an outcome poses a risk to both the translocated type or species and the entire recipient community. In addition, the translocated type itself might become “invasive” or predominant, especially if relocation releases it from a natural enemy or predator. The resulting reductions in diversity caused by dominance of an invasive translocated type could reduce adaptive capacity or resilience (Levin and Lubchenco, 2008) of the community and, in extreme cases, newly predominant types can alter ecosystem structure and function.

The risk of invasion likely increases with the distance of relocation: intercontinental invasions are more frequent than intracontinental invasions (Mueller and Hellmann, 2008), and invasive species have greater invasiveness and greater impact with lower relatedness (measured as phylogenetic distance) to the native community (Strauss et al., 2006). The degree of invasive impact also depends on the novelty of the traits and therefore the ability for the introduced species or type to alter ecosystem processes (Wardle et al., 2011). Invasiveness increases with number of individuals released and number of introductions (Kolar and Lodge, 2001), two factors that also drive relocation success (Fischer and Lindenmeyer, 2000), such that a manager will face a tradeoff between maximizing success likelihood and minimizing invasive risk. In addition, invasiveness has a greater impact on historically isolated communities (Richardson and Pyšek, 2006), which can be particularly relevant to managed relocation, depending on the goal. The most dominant taxa in a database of marine invasive species are crustaceans, mollusks, algae, fish, and annelids (Molnar et al., 2008). Tropical marine systems generally experience lower rates of introduction than temperate systems, but invasive algae can still be particularly harmful (Coles and Eldridge, 2002; Padilla and Williams, 2004).

Accidentally introduced diseases pose a particular risk to coral reefs given that diseases can be a major cause of coral mortality with ecosystem-wide effects, especially in the Caribbean. Additionally, the stress caused both by the environmental conditions being addressed by the relocation, as well as the stress on the coral during relocation, may promote disease transmission. Many coral diseases are not host-specific (Green and Bruckner, 2000) such that relocation could lead to spread to new hosts in a recipient community. The regional heterogeneity in disease incidence, likely due to a mix of environmental variability in thermal anomalies and historic exposure-dependent disease resistance (Rosenberg et al., 2007; Ruiz-Moreno et al., 2012), means that local-scale movement has the potential to enhance disease spread.

Compared to invasiveness of associated organisms and diseases, invasiveness of the translocated coral type or species might pose less of a risk for coral reefs. While invasiveness is difficult to predict from traits (Kolar and Lodge, 2001; Richardson and Pyšek, 2006), it is associated with widespread species (Richardson and Pyšek, 2006) and related characteristics such as dispersal ability (Sakai et al., 2001). In contrast, managed relocation for persistence under climate change typically focuses on range- and dispersal-limited species. There are at least six known species of hard corals that have been unintentionally introduced across oceanic regions: *Tubastrea coccina, Tubastrea micranthus, Tubastrea tagusensis, Fungia scutaria*, *Oculina patagonica,* and *Siderastrea glynni* (Glynn et al., 2016; Coles and Riegl, 2013). The three *Tubastrea* congeners (orange cup corals) that are now considered to be invasive are nonzooxanthellate corals, and the remaining zooxanthellate corals have not spread. The lack of invasive zooxanthellate corals might be due to a lack of propagule pressure; while the majority of marine invasives are from ballast water and aquaculture (Molnar et al., 2008), the majority of tropical marine invasives are from aquaria release (Padilla and Williams, 2004).

Beyond the coral host, the symbiotic zooxanthellae and microbiomes that comprise the coral holobiont also pose a potential to become invasive. Relocation of zooxanthellae and the microbiome associated with a coral host might be a component of managed relocation goals given that stress tolerance and disease resistance are holobiont properties (Baker, 2003; Baker et al., 2004; Berkelmans and van Oppen, 2006; Teplitski and Ritchie, 2009; Ziegler et al., 2017), but spread of these associated organisms to other corals in the target location might alter the co-evolutionary relationships between corals and their symbionts. Genetic evidence suggests the potential for invasive zooxanthellae across ocean basins (LaJeunesse et al., 2016, Pettay et al., 2015).

A risk associated with any translocation is potential damage to reef habitats when corals are collected or when they are placed on new reefs. Collecting can create problems for very rare coral species. An example is the rare pillar coral *Dendrogyra cylindrus*, which has low genetic diversity in the Caribbean, and has seldom been observed to recruit sexually (Marhaver et al., 2015). Collecting a range of genotypes for nursery propagation entails potential risk to the very small natural populations. Another risk might be seen if reef habitats were converted to dedicated coral nurseries at large scales, potentially removing natural populations.

A final risk to ecosystem function is tradeoffs in tolerance to multiple stressors or between stress tolerance and other traits (e.g., growth and reproduction), which can then reduce the performance of the translocated types. On the species level, stress-tolerant morphologies (e.g., massive corals) often have lower growth and reproduction than stress-susceptible morphologies (e.g., branching corals; Darling et al., 2012). As noted above, an unknown is whether increased vigor for one stressor in translocated colonies might lead to decreased vigor for other traits (e.g., potential tradeoff between heat resistance and disease resistance).

Additional risks for each relocation type follow:

Assisted gene flow incurs three additional risks (Aitken and Whitlock, 2013; Weeks et al., 2011). First, assisted gene flow to the wrong place or at the wrong time might incur “gene swamping,” where the input of translocated maladapted genes may dominate over existing better-adapted genes, with a decline in total genetic variation across locations. While gene swamping only occurs above a critical value of migration (i.e., relocation input) relative to selection strength, exceeding this value is more likely with small populations (Lenormand, 2002). Second, assisted gene flow might disrupt local adaptation to nonclimatic factors. For example, relocations might lead to corals spawning at suboptimal times, or a mismatch in spawning between relocated and local corals, which could reduce fitness, fertilization success, or the likelihood of introgression of stress-tolerant genes into local populations. The potential for this mismatch on the spawning time cues and degree of variation in synchrony across locations, varies by species and region (Baird et al., 2009a). Third, assisted gene flow might incur outbreeding depression for hybrids between translocated and native colonies. One transplant experiment of local, nonlocal, and local/nonlocal hybrids does show the potential for reduced survival of hybrid and nonlocal types and therefore either outbreeding depression or disruption of local adaptation in corals on scales of hundreds of kilometers (van Oppen et al., 2014).

Assisted migration incurs the additional risk of interspecific hybridization and loss of a species' identity. Hybridization between introduced species and natives can be a source of invasiveness and a mechanism by which invasives drive biodiversity loss, especially for small, historically isolated populations (Rhymer and Simberloff, 1996; Sakai et al., 2001). This risk is clearly relevant to corals, where hybridization readily occurs (Forsman et al., 2017; Szmant et al., 1997; Vollmer and Palumbi, 2002). How one considers the impacts of hybrids for assisted migration depends on the goal: hybridization may result in loss of a species, but it may aid in maintaining coral-dominated reefs where species is not a concern. See the Managed Breeding section in Chapter 2 for further discussion.

Introduction to new areas does not incur any unique risk not already described above, but it does have an elevated risk of disease and invasive species spread, especially as all known invasive corals involve cross-basin invasions (Coles and Riegl, 2013).

Limitations

A number of limitations might drive failure of relocations to establish ecologically meaningful populations in the new location (i.e., poor survivorship, growth, or reproductive success). Failure of managed relocation might occur due to moving the target organism(s) between the wrong places or at the wrong time, whether due to stochasticity (e.g., a catastrophic event, such as the 2014-2015 back-to-back bleaching events that disrupted a Florida Keys coral restoration project; Lirman and Schopmeyer, 2016), a knowledge gap, and moving without key mutualists (Hewitt et al., 2011). Key knowledge gaps for relocations generally concern what drives species distributions (including the role of species interactions), species responses to novel environmental conditions, local-scale impacts of climate change, natural scales of long-distance dispersal, and the scale of local adaptation (Chauvenet et al., 2013; Gallagher et al., 2015; Hewitt et al., 2011; Kreyling et al., 2011; McLachlan et al., 2007; Rice and Emery, 2003).

The life stage used for relocation (e.g., larval versus fragment release) can influence the likelihood of success and tradesoff with potential risks. Earlier relocation might increase the likelihood of failure due to higher mortality at earlier life stages, while later relocation might increase the risk of invasiveness or gene swamping due to increased establishment likelihood. For corals, earlier life stages can also have greater flexibility in symbiosis (Little et al., 2004), such that earlier relocation might increase the likelihood of shifting to local symbionts (Quigley et al., 2017, 2018a). Shifting to local symbionts might decrease expected stress tolerance if symbionts have different stress tolerance between source and target locations (Ulstrup et al., 2006), but it might also increase relocation success if local symbionts confer adaptation to local conditions. Given that thermal tolerance arises from a combination of coral host, symbiont, and microbiome characteristics (Baker, 2003; Baker et al., 2004; Bay and Palumbi 2014; Berkelmans and van Oppen, 2006; Loya et al., 2001; Ziegler et al., 2017), uncertainty in how relocation affects the symbiont and microbiome contributes to uncertainty in the expected stress tolerance of the translocated type in the target location. The earliest possible relocation, not yet feasible but in development, is at the gamete stage with spawning in captivity and then release of fertilized eggs (Craggs et al., 2017). Using local eggs with nonlocal sperm in assisted gene flow would eliminate the risk of accidentally introducing diseases or invasive species from associated organisms, as well as reduce the risks of gene swamping and disruption of local adaptation to nonclimatic factors. The translocated hybrids would likely be more adapted to nonclimatic conditions, but might also confer lower stress tolerance, as compared to translocating fully nonlocal types.

In terrestrial translocations for general conservation purposes (e.g., reintroductions within historical ranges), about half of the cases with sufficient data to evaluate efficacy are successful (Dalrymple et al., 2012; Dodd and Seigel, 1991; Fischer and Lindenmeyer, 2000), and coral reintroductions exhibit analogous success rates (Young et al., 2012). Therefore, both irreducible (present regardless of knowledge) and reducible (knowledge-dependent) uncertainties may limit translocation success (Ladd et al., 2018). Ongoing climate change can magnify such uncertainties. Drivers of translocation success in terrestrial systems include using wild (rather than captive) sources, large releases, and removal of the original causes of decline (Fischer and Lindenmeyer, 2000). In corals, removal of causes of decline might include reduction in nutrient, sediment, and other pollutant loads as well as restoration or protection of ecologically functional herbivorous fish and invertebrate populations (Ban et al., 2014; Pandolfi et al., 2003; Wilkinson, 1999; Zaneveld et al., 2016). Similarly, translocation success may benefit from interventions that decrease exposure to climate stresses. Reduction of such local stressors might also reduce the risk of disease spread (Green and Bruckner, 2000; Rosenberg et al., 2007).

In summary, a number of challenges can limit the success of managed relocation, including the risks and infrastructure needs described in other sections of the chapter (Table 4.1). In addition to the cost of a failed project, failure could represent loss to the source population, although nursery grow-out techniques that develop larger populations from small fragments mitigate such costs (Lirman and Schopmeyer, 2016). Many of these limitations depend on the management approach (e.g., quarantining of fragments or relocation of gametes reduce risks of non-native species and pathogens) or knowledge availability (e.g., increased knowledge of relative plastic and genetic, and relative coral, zooxanthellae, and microbiome contribution to thermal tolerance can reduce the likelihood of no conference of stress tolerance between source and target locations), while others are irreducible (e.g., storm events following relocation).

Infrastructure

Managed relocation efforts and activities are time and labor intensive. Extensive infrastructure including boats, seawater facilities, and recipient site preparation are critical to success. The collection and transportation of corals can result in colony mortality and require careful planning to reduce handling, transit time, and physical damage. Containers with ample water volumes, temperature control, and circulation/aeration are essential for the survival of colonies and fragments collected from field sites (Precht, 2006). When moved to and maintained in land-based facilities, flowthrough or recirculating seawater systems are needed to allow collected corals to recover from the stress of collecting, and to support continued growth and in the case of translocating gametes, undergo successful gametogenesis and spawning or planulation. Such facilities require dedicated technical staff and redundancy in pumps and the electrical supply to insure against losses. *In situ* collecting and outplanting activities are also labor intensive and require numerous SCUBA divers and all of the associated operational and safety equipment. Volunteers can be used to supplement professional staff, but they require substantial training and supervision.

Beyond the technical infrastructure, additional requirements arise from gathering the data necessary for the managed relocation decision-making process and monitoring. Aspects of the decision-making process that require site, system, or species-specific data include identification of target species, locations, and timing of relocation as well as assessment of risks such as accidentally invasive species and pathogens.

TABLE 4.1 Summary of Limitations to Managed Relocation

Limitation Category	Limitations
Knowledge requirements	• Ability to identify stress-tolerant types/species, vulnerable types/species, or factors in which to maximize diversity • Ability to identify source and target locations based on SDMs, monitoring of coral trends, or other relevant data • Ability to distinguish translocated type from hybrids or cryptic species • Amount of natural connectivity between source and target locations • Thresholds in target population size, target population diversity, and overall coral density for transplant survival and reproductive success
Technical requirements	• Coral nursery infrastructure • Resources for large-scale out-planting and monitoring
Sources of failed relocation	• Ongoing local stressors such as sedimentation, pollution, and overfishing • Local environmental factors (both abiotic—e.g., salinity, illumination—and biotic—e.g., endosymbtionts, exosymbionts) not appropriate • Stochastic high-mortality event, such as a storms, following relocation • Limited availability of habitat and appropriate substrata for recruitment at target location • Stress tolerance at source location not conferred to target location due to unanticipated plasticity or contribution of zooxanthellae or microbiome to tolerance
Risks	• Potential for relocation of non-native species • Potential for relocation of non-native disease • Potential for relocated species or type to become invasive • Altered ecosystem structure and function • Unanticipated tradeoffs between tolerance to multiple stressors or between stress-tolerance and other traits relevant to coral persistence • For assisted gene flow: outbreeding depression, gene swamping, and disruption of local adaptation (especially for relocation to small populations)

5

Environmental Interventions

While mitigation of global carbon emissions is the obvious global solution to climate change, even limiting human-induced surface warming to 2°C is unlikely to protect most coral reefs from an increased frequency and severity of bleaching events (Frieler et al., 2013). Even if biological and ecological interventions are able to enhance the thermal tolerance of some coral species by 1°C, predicted emissions scenarios in the coming decades may still lead to temperatures that exceed the thermal tolerance of most species, even under the Representative Concentration Pathway 2.6 by the IPCC (e.g., Anthony et al., 2017; Lough et al., 2018). Therefore, strategies that employ a portfolio of coordinated interventions including local cooling, shading, and amelioration of ocean acidification (OA) in combination with biological and ecological interventions may be necessary for building climate resilience in coral reefs.

A number of candidate interventions may provide such local, and in places regional, relief of climate-driven stress on reef ecosystems. These operate on a scale from microhabitats (meters) to potentially subregions (hundreds of kilometers) and serve a key purpose: reduce temperature and light stress during summer warming events where coral bleaching risk is significant (Eakin et al., 2009; Hoegh-Guldberg, 1999) and alter the chemical environment around coral reefs to reduce acidification impacts. Because OA can exacerbate thermal stress (Albright et al., 2016; Anthony et al., 2008; Kroeker et al., 2013; McLeod et al., 2013; Reynaud et al., 2003), efforts to alleviate OA locally may also indirectly lower stress from climate change. These interventions include atmospheric, sea surface, and water column reflection or absorption of light, advection of cooler reef waters around reefs, and lowering of water acidity and increasing water acid-buffering capacity. While the biological and ecological interventions considered in previous chapters act to enhance stress tolerance, the environmental interventions considered here all act to reduce or prevent stress exposure directly. In theory, if these environmental interventions can be made sufficiently effective at scale, then they can buy time for biological and ecological interventions to be developed further.

Here we review such interventions in light of projected climate change scenarios. Local cooling and shading interventions are in essence engineering solutions constrained by logistics, resources, and efficacy. Abiotic interventions to address OA fall in the category of engineering solutions using physical and/or chemical interventions that directly alter the ocean carbon chemistry towards higher pH and aragonite saturation state (Ω_a). Biotic interventions take advantage of the natural abilities of some marine species or biological communities to draw down CO_2 and/or shift the seawater chemistry in a direction that ameliorates OA. The strengths of these interventions are in targeted asset protection, rather than broadscale prevention, at least without up-scaling of effort and potential risks. Such local- and regional-scale interventions are distinct from geoengineering initiatives that manipulate the atmosphere in an attempt to regulate the Earth’s global climate (e.g., Crutzen, 2006; Ricke et al., 2010; Robock et al., 2008a, 2008b).

SHADING OF CORAL REEFS

What It Is

Shading interventions are those that reduce the exposure of coral reefs to solar radiation, with the purpose of reducing light incidence and/or lowering water temperatures. Pacific coral reefs that were under cloud cover in the summer of 1998 avoided bleaching (Mumby et al., 2001). Bleaching risk has also been lowered by volcanic clouds (Gill et al., 2006) and marine turbidity (Cacciapaglia and van Woesik, 2016; Oxenford and Vallès, 2016). Engineered options for shading coral reefs may occur either in the atmosphere or in the water column over the reef. Induced cloud formation and/or brightening has been proposed as a means for atmospheric shading. Marine shading has been suggested to include increased turbidity, shading layers, microbubble ocean whitening, and wave lensing reduction. For each of the shading interventions that are not based on a fixed structure, the advection of the substance or effect into and out of the target area needs to be considered when evaluating scale and effectiveness.

Benefit and Goals

Shading of the atmosphere and ocean surface on or near coral reefs during warm summers can reduce bleaching risk by alleviating both heat stress and light pressure. The role that both heat and light stress play in coral bleaching is described in Chapter 1. Shading may cool the water column, and thereby cool the water around reef organisms. For example, if 30% of the sun's irradiance can be absorbed or scattered in the atmosphere over a coral reef at noon during summer, it would lower the energy in the system by around 10 MJ m^{-2} d^{-1} (e.g., Masiri et al., 2008). Additionally, because light is a co-factor in the coral bleaching process (e.g., Lesser and Farrell, 2004), shading will directly lower coral bleaching risk. This is the rationale for NOAA's light stress product,[1] which helps account for the total environmental stress that causes coral bleaching.

How to Do It

Below we present briefly the technical capability and challenges of each category of intervention. Generally, shading can occur in the atmosphere, at the water surface, or in the water column, at diminishing scale, respectively.

Atmospheric shading

Clouds and aerosols in the atmosphere absorb and scatter solar radiation (Lacis and Hansen, 1974). Natural aerosols resulting in part from ocean primary productivity and ocean surface spray are key drivers of cloud formation and cloud albedo (McCoy et al., 2015). Artificially induced shading can be accomplished by introducing reflective particles in the upper atmosphere (above the troposphere) thereby inducing low-altitude cloud formation (Latham et al., 2012). Stratospheric cooling can be accomplished by injection of sulfur aerosols, akin to the natural process of volcanism (Crutzen, 2006), and this has been suggested as a possible strategy to mitigate coral bleaching (Zhihua et al., 2018).

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[1] https://coralreefwatch.noaa.gov/satellite/lsd/index.php

Low-altitude cloud formation above the air-sea boundary layer can also be promoted by seeding with aerosolized seawater particles near the marine surface (Latham et al., 2012). On a global scale, the resultant brightening, and hence reflection of solar radiation, can reduce globally averaged incoming radiant energy by up to 4.8 W m^{-2} at the top of the atmosphere (Alterskjær et al., 2012). This can produce a cooling effect sufficient to mitigate warming equivalent to a doubling of the atmospheric CO_2 concentration relative to pre-industrial levels (Latham et al., 2013). However, sky brightening could potentially be targeted to specific reef areas to promote cooling (Latham et al., 2012) and reduce incident light during thermal anomalies. Previous efforts to model sky brightening have focused on areas where low marine clouds are abundant and would interact with injected particles (indirect brightening; Latham et al., 2012). However, more recent modeling suggests that injected particles themselves have a strong brightening effect (direct brightening; Ahlm et al., 2017), suggesting that even regions without abundant marine clouds, or when marine clouds are absent during bleaching conditions, could benefit from low atmosphere particle injection. Although typically referred to as “marine cloud brightening,” this means that “marine sky brightening” is a more appropriate term for sea spray climate or reef protection engineering (Ahlm et al., 2017).

Marine shading

Induced turbidity: Suspended particulate matter, generally referred to as turbidity, filters light in the water column, hence reducing benthic irradiance (Devlin et al., 2008; Falkowski and Raven, 1997). High turbidity on coral reefs is generally considered a stress factor as it can lead to a negative energy balance for autotrophic organisms, and settling particles may smother coral reef organisms (Fabricius, 2011; see Chapter 1 for further discussion). However, coral bleaching risk may be reduced by low or moderate turbidity (Anthony et al., 2007; Cacciapaglia and van Woesik, 2016) and potentially other reflective surfaces in marine waters (Seitz, 2011). Also, because suspended particulate matter may represent an alternative nutrient and energy source, it has the potential to lower mortality risk associated with bleaching (Anthony et al., 2009; Connolly et al., 2012).

Shading layers: Both fixed physical shades, such as surface shade cloths (Rau et al., 2012), and temporary surface films have been used or proposed to reduce incident light on corals. Shade cloths have been shown to reduce bleaching in *Acropora muricata*, *Pocillopora damicornis,* and *Porites cylindrical* in American Samoa (Coelho et al., 2017). Shade cloths were used at a small scale (tens of meters) to reduce light stress on high-value reefs on the Great Barrier Reef (Rau et al., 2012). Also on the Great Barrier Reef, a project is trialing a reflective polymer surface film as a potential tool to shade coral reefs during summer doldrums[2]. The buoyant, monolayer polymer film consists primarily of calcium carbonate ($CaCO_3$) and is reported to be biodegradable and innocuous. Results of early trials in the Sea Simulator at the Australian Institute of Marine Science indicate that the film can reduce surface penetration of solar irradiance by up to 30% in calm sea states.

Microbubble ocean whitening: Seitz (2011) has proposed the use of very fine bubbles or “highly dilute micron-radius hydrosols” to brighten surface waters and reflect light away from

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[2] See announcement at https://www.barrierreef.org/latest/news/reef-sun-shield-trials-show-promise-to-prevent-coral-bleaching

the sea bed. In principle, this is the water-column equivalent to cloud brightening, and at fine local scale. The technique is proposed to reduce the amount of energy reaching the seabed by up to 100 W m^{-2} and at relatively low cost (Seitz, 2011).

Wave-lensing reduction: Wave-lensing is the focusing and defocusing of incident light on the ocean's surface by the complex surface topography caused by waves. Wave lensing causes highly transient light flickering (within seconds) on shallow ocean floors, with order-of-magnitude increases and decreases in irradiance (Veal et al., 2010). This can be reduced over small areas by breaking up the water surface with techniques such as seawater sprinklers. The effect is only a modest decrease in mean downwelling photosynthetically-active radiation and UV irradiance, but reduces irradiance variability. However, Veal et al. (2010) concluded from experiments that shallow-water corals are not negatively impacted by wave lensing at bleaching temperatures; therefore, this potential intervention will not be discussed further.

Current Feasibility

Techniques that shade coral reefs to cool water and lower photo stress are at various stages of feasibility that largely relate to their intended or potential scale. Atmospheric approaches (i.e., marine sky brightening) at the regional and local scales still need further technical development to be ready for implementation (Latham et al., 2012). Increased turbidity, shading layers, and ocean whitening could all technically be implemented now on small scales (less than 1 km). However, while their effectiveness can be derived theoretically, they are untested as operational solutions.

Potential Scale

One advantage to marine shading manipulations for near-term thermal stress (see Frieler et al., 2013) is that they can be targeted in time and space to areas under acute thermal stress. However, the cost-benefit ratio of some techniques may be too high to scale up to regions or whole reefs. An example is shading screens or structures; while they are effective at, for example, the scale of a tourism pontoon, the infrastructure required to scale up becomes both cost prohibitive and logistically infeasible. Some techniques may also be limited in spatial and temporal scale because of the dissipation of the effect after application. For example, surface polymer films may be advected away from a reef by currents after application and therefore require monitoring and maintenance during a potential bleaching event. Atmospheric shading from marine sky brightening and marine whitening, on the other hand, could be scaled up to local and regional spatial scales with few constraints. The limiting steps here are integrated systems for coordinated application, ideally linked to satellite mapping of cloud covers, computer models of winds and weather, and network control of dosing arrays.

Risk

A key risk from shading is light reduction to photosynthetic organisms, including corals. In deeper or turbid waters, phototrophic organisms may already be near the compensation point where photosynthesis is balanced by respiration. This can cause shallowing of the depth limit of corals and phototrophic organisms, such as seagrasses, under the area shaded (Latham et al.,

2013) or complete restriction of some organisms from areas that are turbid (Bessell-Browne et al., 2017). For any strategy apart from fixed shading structure, it would be difficult to control the boundaries of the affected area in turbulent atmospheric and oceanic waters because of advection. Sedimentation is a common stressor on coral reefs and its use as a shading intervention would need to consider any unintended side effects such as enrichment with particulate nutrients or the smothering of benthic organisms as particles settle onto the seafloor. Bubbling would alter the gas balance, including CO_2, in surface waters and such alteration of water chemistry could have risks if, for example, surface waters were enriched with CO_2. Importantly, however, the downside risks of any of these shading techniques need to be considered in the context of the damage they may prevent during an acute heat wave. In other words, if shading can be kept short, their downside relative to upside risks may be both low and manageable.

Other risks from aerosol injection in the atmosphere include the impact of settling salt particles and changes in precipitation on adjacent habitats (e.g., including commercially and socially valuable areas such as agricultural lands). This review does not focus on global climate engineering, but more locally on atmospheric engineering specifically protective to coral reefs. However, the risks of shading may apply equally to global or regional/local strategies.

Another risk of shading (and also cooling, described in the next section), could be the reduced scope for natural adaptation to thermal stress. In other words, lowering local thermal stress by shading may limit a pathway for acclimation. If shading or cooling interventions cannot be sustained, unhardened coral fauna could face rapid onset of thermal stress. Effectively, once a cooling or shading regime is implemented in an area or a region, the effort requires sustained commitment. Last, and importantly, interventions to reduce heat and light exposure and support persistence are only capable of buying time while global mitigation efforts seek to stabilize the climate.

Limitations

The shading approaches are largely limited by scales of operation. Shade sails at high-value dive sites on the Great Barrier Reef were highly localized (meters), and the idea has not been pursued because their cost-benefit ratio is too high. Other techniques might be limited by their efficacy. For example, marine polymer films can reduce incident light by 30%, but shading experiments suggest that even at 50% and 75% light reduction they do not protect corals from bleaching during severe heat waves (Coelho et al., 2017). Another consideration is direction and rates of atmospheric and marine fluid flow, which limits the area affected and the residence time of the effect (Mark Baird, presentation to the committee).

Infrastructure

The infrastructure needed to support marine shading is labor intensive and potentially costly. Small-scale interventions, such as physical barriers and microbubble generators, require boats for installation of equipment and potentially in-water manipulation by divers. Microbubble generators and methods to increase turbidity (e.g., sediment resuspension) require energy to drive mechanical pumps, agitators, or similar tools and this generates logistical challenges in the marine environments. Local, regional, or larger-scale sky brightening requires boats with pumping and dispersant systems. These boats may be autonomous with periodic human maintenance or constantly manned vessels.

Monitoring for efficacy and control of negative environmental impacts requires a different set of infrastructure. At the reef level, established methods of in-water direct and autonomous monitoring of corals will be needed to assess the efficacy of the intervention. Monitoring will also be needed for maintenance of the intervention itself. For spatially-fixed interventions, such as shade cloths, this requires some on-site or remote monitoring. For interventions that advect in water or sky, monitoring is needed to assess where to continue application to alleviate heat stress. Polymer films and microbubbles may require water sampling to establish the dispersal and lifetime of the polymer and bubble particles, unless the film can be detected from airborne sensors. Sky brightening may be detected from satellites or atmospheric sensors, but there is an issue of a standard from which to judge efficacy (Robert Wood, presentation to committee).

MIXING OF COOL WATER

What It Is

Thermal reduction can be accomplished by a process that replaces or dilutes warm water with cooler water. Active methods of bringing in cooler waters to thermally stressed reefs are possible in areas with access to deeper, cooler waters. These methods include mechanical pumps or self-sustaining processes (such as the differential in temperature between the depths and surface waters) to create artificial upwelling to replace shallow and warm with deeper and cooler water.

Benefit and Goals

The goal of cool water mixing is thermal stress reduction sufficient to prevent or lower the risk of coral bleaching. In natural systems, this is analogous to reduction of thermal stress by upwelling and enhanced vertical mixing (Glynn, 1996; Riegl and Piller, 2003).

How to Do It

Most of the experimental work on artificial upwelling has been done in the context of aquaculture and ocean fertilization (Pan et al., 2016). Pulling up of deep water can be accomplished through active methods, such as pumps and air lifts driven by nonrenewable energy (municipal electricity and fossil fuels) and renewable energy (e.g., ocean wave energy), or passive methods that take advantage of thermal and salinity differences between layers to generate a self-sustaining flow of water.

Current Feasibility

While technically feasible to create mechanisms for artificial upwelling, the efficacy of these approaches has not yet been tested fully. Underwater fans have recently been deployed in a trial phase on the Great Barrier Reef under the Reef Havens project.[3] The intent of the program is to bring up cooler water from depth to shallow waters and under doldrum conditions to provide local relief of peak sea surface temperature. This program targets selected, high-value reefs used by tour operators. Only one small-scale example of bringing up cool water to alleviate bleaching has been demonstrated.[4]

Potential Scale

Current initiatives such as the Reef Havens fan project are at the scale of one to a few hectares only. While it is conceivable that larger pump or fan systems can be made operational in places where there is access to cooler water at depth, the ability to scale up will be limited by infrastructure requirements. Like shading, cool water mixing is a temporary stress relief that can be focused during periodic times of environmental stress.

Risk

One of the technical risks associated with the pumping of deep, cooler waters to coral reefs in shallow water is that such artificial upwelling potentially leads to both nutrient and CO_2 enrichment, exacerbating algal growth and OA (e.g., Feely et al., 2008; Leichter et al., 2003; Manzello, 2010).

Limitations

The surface mixing of cool deep water and warm surface water needs to be considered to understand the size of the water mass that needs to be cooled. The cooling load is the amount water at a lower temperature and density needed to reduce the temperature of another warmer water mass at a given temperatures and density, and this then needs to be scaled to a reef (Mark Baird, presentation to committee). For the method to be effective, the reef cooling load needs to be determined *a priori*. This means taking account of spatial variability in processes that determine advection and residence time of the cooled water mass, such as local wind, distance to reef edge, and depth. Also, depending on the geographical and oceanographic setting on and around coral reefs, very deep water (more than 30-50 m) may need to be pumped to achieve more than 1°C cooler water at the surface (Furnas and Mitchell, 1996). Thus, the cooling effect is dependent on a high degree of reef-specific characteristics and may need to be applied on a reef-to-reef basis. In addition, because the present mechanisms to generate upwelling are small- cale and constrained by source water, the application of water cooling will likely be localized and not regional.

Infrastructure

The infrastructure needed for reef water cooling includes boats, pumps, and divers. Reducing the environmental impact of deep installations will need to take into account deeper water ecosystems and, thus, in many location will require *in situ* biological assessments.

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[3] http://rrrc.org.au/reef-havens/

[4] http://www.climatefoundation.org/coral-reef-cooling.html

ABIOTIC OCEAN ACIDIFICATION INTERVENTIONS

What It Is

Abiotic OA interventions at the local reef scale act directly on the carbon chemistry of the seawater flowing over reefs. Interventions can be either chemical, involving the addition of a strong base to elevate pH or by interacting with the reef limestone, or physical, for example stripping CO_2 from the water column.

Benefit and Goals

The fundamental goal of any OA amelioration technique is to shift the seawater carbon chemistry toward an increasing pH level (Raven et al., 2005; Figure 5.1a) and more saturated aragonite saturation state (Kleypas et al., 1999). While pH is a key indicator of OA, the range of biological processes affected by changes in the ocean carbon chemical system are more fully represented by Ω_a, which is a measure of the amount of carbonate ions in solution (Kleypas et al., 2006). This is critical because some OA manipulation techniques will affect pH but may only have limited effect on the carbonate system (Gattuso and Lavigne, 2009; Figure 5.1b).

How to Do It

A number of different physical and chemical approaches show varying promise. We provide five examples to illustrate physical, chemical, and combined techniques.

Bubble stripping: The use of bubble streams with low CO_2 partial pressure to remove CO_2 from seawater builds on the principle that CO_2 in air equilibrates with CO_2 dissolved in seawater (Zeebe and Wolf-Gladrow, 2001). Modeled experiments indicate that CO_2 stripping using plumes of fine bubbles in a shallow-water environment can lower the CO_2 partial pressure by around 20% over a 2-hour period (Koweek et al., 2016). Importantly, the effectiveness of CO_2 removal is a direct function of the CO_2 partial pressure in the bubble stream and the size distribution of bubbles. Challenges associated with this technique are adequate CO_2 stripping of the bubble stream and the fact that CO_2 is displaced from ocean to atmosphere.

Addition of strong bases: Manipulating pH directly with the addition of a strong base (e.g., NaOH) forces a shift in the relative distribution of pCO_2 and the carbonate ion concentration (Figure 5.1a; Albright et al., 2016; Riebesell et al., 2010). While pH is increased, no CO_2 is removed from the system. Again, exact dosing to match the environmental pH is challenging in a variable environment and sufficient dosing is a supply issue.

Addition of limestone: The dissolution of $CaCO_3$ powder has been proposed as a mechanism to enhance CO_2 uptake by the global ocean, and further as an avenue for limiting ocean acidification (Harvey, 2008). The technique builds on the principle that added $CaCO_3$ ions consume hydrogen ions, thereby elevating pH and aragonite saturation state. It does so primarily by elevating the total alkalinity (Figure 5.1b). Two key challenges of the technique at any scale are (1) to match the limestone dosing with environmental chemistry, and (2) to source material adequately and sustainably.

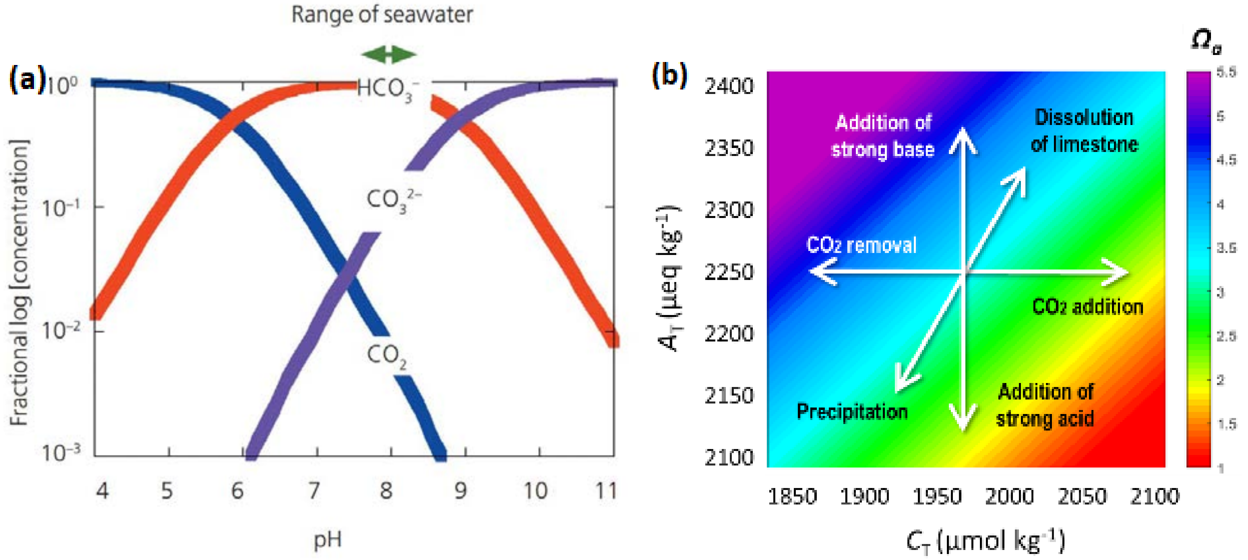

FIGURE 5.1 (a) Relative distributions of dissolved carbon dioxide (CO_2), carbonate ions (CO_3^{2-}) and bicarbonate (HCO_3^-) as a function of seawater pH. The graph illustrates the large scope for aragonite saturation state changes driven by changes in CO_2 and CO_3^{2-} within the relatively narrow pH range of seawater (7.5–8.5) likely to occur in coral reef waters now and under future climate scenarios. SOURCE: Raven et al., 2005. (b) Functional relationship between the total concentration of dissolved inorganic carbon (C_T), total alkalinity (A_T) and aragonite saturation state (Ω_a, colorbar). Arrows indicate how interventions that add or remove CO_2 affect aragonite saturation. Furthermore, processes that lead to $CaCO_3$ dissolution or precipitation will increase or decrease Ω_a via alkalinity changes, respectively. In essence, while OA is the addition of CO_2 from the atmosphere, interventions that act to ameliorate OA need to remove CO_2 and/or promote an increase in alkalinity. SOURCE: Based on information in Gattuso et al., 2010.

Accelerated weathering of limestone: This technique is a variant of the addition of limestone, but involves the use of CO_2 to create a local environment of low pH around a $CaCO_3$ source. The dissolution of limestone in turn leads to increased total alkalinity. The outcome is a net increase in aragonite saturation state (Rau et al., 2007) along the “dissolution of limestone” axis in Figure 5.1b. This operates at a small scale in the calcium reactors used in maintaining alkalinity levels in aquariums.

Electrochemical splitting of calcium carbonate: Here, $CaCO_3$ (for example using deposits from rubble banks) is split between a cathode and an anode, forming calcium dihydroxide ($Ca(OH)_2$) at the cathode and carbonic acid (H_2CO_3) at the anode. Reactions between $Ca(OH)_2$ and dissolved CO_2 then produce dissolved calcium bicarbonate ($Ca(HCO_3)_2$) (Rau, 2008). While the method shows promise, questions arise around the economics and scalability of electrochemical approaches.

Current Feasibility

All five methods above are feasible now at small scale. Aeration is already being used to remove pollutants in wetlands (Ouellet-Plamondon et al., 2006). Logistical constraints here would be the ability to pump enough CO_2-stripped air into the water body upstream of the target coral reef. Injection of air with atmospheric-level CO_2 will not ameliorate ocean acidification on reefs exposed to oceanic currents but may in areas where metabolic processes temporarily lower pH and Ω_a (Koweek et al., 2016). Similar logistical constraints would apply to the other techniques, but rather than injecting air at the target site, the dosing of limestone powder, strong bases, CO_2, or power present further complications and risks.

Potential Scale

All methods above operate at the local scale only—kilometers at best. The reality is that ocean acidification is an escalating global phenomenon. Furthermore, some coral reefs are exposed to vast volumes of oceanic water every day. CO_2 extraction or chemical conversion would require consistent and homogeneous dosing of large amounts of CO_2-stripped air, limestone, or strong bases. Even at such a small local scale, the resourcing, infrastructure, and maintenance required to consistently counteract ocean acidification would likely be unsustainable.

Risk

Bubble streams may carry the least risk because only air is injected into the marine environment. The modeling study by Koweek et al. (2016) was applied to a shallow, coastal embayment where metabolic processes can drive pCO_2 levels to more than twice that of the atmospheric concentration during the night (Albright et al., 2015; Shaw et al., 2012). Under such circumstances, bubbling with unmodified atmospheric air can lower pCO_2 in the marine environment with relatively low risk. However, if CO_2 first needs to be removed from the airstream using chemical techniques (House et al., 2011) then environmental risks (e.g., spills) and cost are likely to increase.

Direct dosing with limestone or strong bases could represent high risk. For example, the spatial and temporal variability of the physiochemical environment of reef environments (e.g., Mongin et al., 2016b) means dosing in space and time will need to be anticipatory as well as responsive.

Limitations

Scale, logistics, resources, and infrastructure represent major constraints. In general, OA amelioration is limited to local intervention where the environmental setting (oceanography, hydrodynamics, and bathymetry) is such that flow direction is predictable, depth is shallow, and/or reefs are in an embayment where the seawater carbon chemistry can be modified cost efficiently. As carbon-removal techniques become more effective and cost-efficient (House et al., 2011), local control of seawater carbon chemistry over coral reefs might become more feasible, but will still be limited to the local scale and to a subset of oceanographic settings.

Infrastructure

The exact dosing of chemicals, air or limestone to reefs in such a way that the marine carbon chemistry can be kept within a range that favors coral survival, growth and reproduction requires precision technology on a massive scale. Even technologies that attempt this at the scale of tens of meters in aquarium, field or large laboratory settings demand automated sensing, control and dosing equipment typically at the scale of hundreds to millions of dollars (Dove et al., 2013; Kline et al., 2012).

SEAGRASS MEADOWS AND MACROALGAL BEDS

What It Is

Seagrass meadows and macroalgal (commonly known as seaweed) beds have the potential to drawdown CO_2 concentrations and elevate Ω_a in shallow-water environments on or adjacent to coral reefs, in effect serving a localized carbon-sequestration function. The draw-down of CO_2 by benthic primary producers is part of the carbon cycle in the oceans and may also play a role in global carbon sequestration (Krause-Jensen and Duarte, 2016).

Benefit and Goals

The motivation behind this inquiry into seagrasses and macroalgae as OA management tools is that waters over some seagrass beds have significantly higher pH and Ω_a than oceanic waters during periods of high productivity, suggesting that natural OA refugia exist, at least temporarily (Manzello et al., 2012). These observations raise the idea that active promotion or spatial conservation planning of seagrass meadows or macroalgal beds near coral reefs could be an opportunity to identify or develop such refugia as part of an intervention strategy to help sustain coral reefs under climate change.

Seagrass meadows may be more effective in elevating Ω_a than macroalgal beds (Manzello et al., 2012; Unsworth et al., 2012). This is partly because seagrass rhizomes stimulate carbonate dissolution in the sediment pore water (Burdige and Zimmerman, 2002), hence elevating seawater alkalinity and, as a consequence, Ω_a. Seagrasses can also store carbon for longer periods than macroalgae in their rhizomes, which macroalgae lack. Seagrasses therefore both draw down CO_2 and increase alkalinity, thus driving up Ω_a analogous to the combined macroalgae-sand scenario above (Figure 5.2e,f). Also, because seagrasses are carbon-limited, whereas macroalgae are not, the effectiveness of seagrasses in elevating Ω_a may increase with OA (Palacios and Zimmerman, 2007).

Contrary to seagrasses, some macroalgae are a food commodity used in aquaculture or farming (Msuya et al., 2007) and biofuel production (Wei et al., 2013). Macroalgal farming in areas adjacent to coral reefs may both generate a revenue stream that more than pays for the cost of the intervention, and maximize net Ω_a increase by removing the fixed carbon before it breaks down. Without removal, decomposing macroalgae increase community respiration (Falter et al., 2011), reintroducing CO_2 into the system, thereby lowering the efficacy of the approach.

How to Do It

Local reversal of OA using benthic primary producers works on a set of simple processes and objectives. Specifically, the aim is to increase Ω_a, or counteract its decline, locally. This can be achieved via two key avenues. The first is to increase the ratio of benthic photosynthesis to respiration in areas upstream of the target coral reef (Anthony et al., 2011; Kleypas et al., 2011). The second avenue is by promoting net $CaCO_3$ dissolution, as opposed to calcification, in upstream areas or on the reef itself (Anthony et al., 2013). The results of these biotic processes bear resemblance to the abiotic processes discussed above. The first process can be achieved directly by macroalgal beds or seagrass areas upstream of the target coral reef.

The extent to which these processes will work to achieve the objective (elevating Ω_a of coral reef waters), depends on the extent to which photosynthesis exceeds respiration and dissolution exceeds calcification in the upstream area. A scenario that maximizes Ω_a is captured by the following hypothetical: A coral reef is situated directly downstream of a large shallow area of a dense macroalgal bed (or seagrass meadow) during the day, and directly downstream of a large shallow area of reef sand with minimal content of organic matter during the night. The day/night shift in upstream benthic type is here assumed to be driven by tides and/or a shift in wind direction.

This near-optimal situation can be demonstrated by the results of flume experiments by Anthony et al. (2013) that examined carbon fluxes in six different benthic groups from shallow reef environments around Heron Island on the southern Great Barrier Reef (Figure 5.2). The dense macroalgal bed in the experimental flume increased Ω_a by nearly one unit per hour (at 1 m depth) under high-CO_2 concentrations and high-flow conditions and half a unit under low flow (Figure 5.2f). Half of this gain was offset by algal respiration at night. The daytime gain by macroalgae could, in this experiment, fully offset the Ω_a drop due to coral calcification during the day (Figure 5.2a). Calcifying macroalgae such as *Halimeda* are less effective in elevating Ω_a than noncalcifying macroalgae because their calcification also draws down alkalinity (Figure 5.2c; see also Chisholm and Gattuso, 1991). At night, dissolution of crustose coralline algae (Figure 5.2b) and coral sand (Figure 5.2e) contributed most positively to Ω_a under the acidified scenario. However, respiration by organic matter in the sand used in this experiment offset the Ω_a benefit from dissolution. In summary, the example illustrates that a dense upstream macroalgal bed the size of the coral reefs (areas are constant across benthic groups in Figure 5.2) can fully offset coral-driven Ω_a decline during the day. Also, water flowing from a large area of sand (e.g., a lagoon) at night may offset night-time Ω_a decline driven by night-time coral calcification and respiration. See Kleypas et al. (2011) for an additional case study.

The environmental context of the use if seagrass meadows or macroalgae as an OA management intervention is important to consider in implementing the strategy:

1. **Water depth.** The drawdown of seawater CO_2 will only be effective in shallow water because the ratio of photosynthesis to respiration, and hence CO_2 fixation versus release, generally declines with water depth (Barnes and Chalker, 1990), specifically below the point of photo-inhibition (Hoogenboom et al., 2006, 2009).
2. **Water residence time.** While fast-moving water promotes the exchange of CO_2 (and other chemical species) and the biota (Mass et al., 2010; Shashar et al., 1996), slow-

moving water allows for a longer period of CO_2 exchange between the benthic primary producers and the overlying water column.

3. **Seagrass or macroalgal density.** Optimal density will be a compromise between maximizing the three-dimensional surface area of photosynthesizing thallus or leaf surface per square meter of seabed and the extent to which crowding does not impede CO_2 exchange.
4. **Fate of the fixed carbon.** If seagrass or algal decomposition is allowed to occur within the management area, then the net Ω_a change may be zero. A harvesting protocol can help increase efficacy (Mongin et al., 2016a), as can hydrodynamic settings where detritus is transported into deep water (Krause-Jensen and Duarte, 2016). If a harvesting strategy is part of an algal farm, then social and economic benefits can promote sustainability and upscaling.
5. **Geographical, oceanographic, ecological, geomorphological, and meteorological setting.** A large number of processes will need to be aligned for biological OA management to be possible. Coral reefs directly exposed to a strong flow of oceanic water cannot be managed for OA locally. From a planning perspective, strategies that start by identifying natural OA refugia (Manzello et al., 2012) are likely to have higher efficacy than attempting to create such an alignment of factors by design or via engineering.

Current Feasibility

The main barrier to successful local OA management using seagrasses and macroalgae is the alignment of environmental factors that can transfer the benefits of OA reversal by the primary producers to the coral reef with maximum efficacy. Inshore settings where seagrasses are already elevating Ωa naturally above levels of the open ocean demonstrate feasibility and readiness (Manzello et al., 2012). In other settings, feasibility needs to be addressed with a more general question: is the setting such that the water body "treated" by the primary producers flows over the coral reef consistently? If so, does the Ωa increase in that water body more than exceed the Ωa decline caused by the open-ocean OA influence and by reef calcification and metabolism?

Dynamic modeling allows for the formal design and quantitative testing of the efficacy of a local OA management solution. Specifically, linked biogeochemical and hydrodynamic models resolve local and potentially regional oceanographic drivers and their interaction with the benthic ecosystems (Schiller et al., 2014; Mongin et al., 2016b).

Potential Scale

While ocean acidification is driven predominantly by atmosphere-seawater exchange of CO_2 across the global oceans, the role of benthic processes and coastal influences increases as one moves into shallow water and toward coastlines (Duarte et al., 2013). In shallow water, and especially coastal environments, the carbonate chemistry of seawater is modified by benthic biogeochemical processes operating over multiple spatial and temporal scales (Albright et al., 2015, 2016; Takeshita et al., 2018).

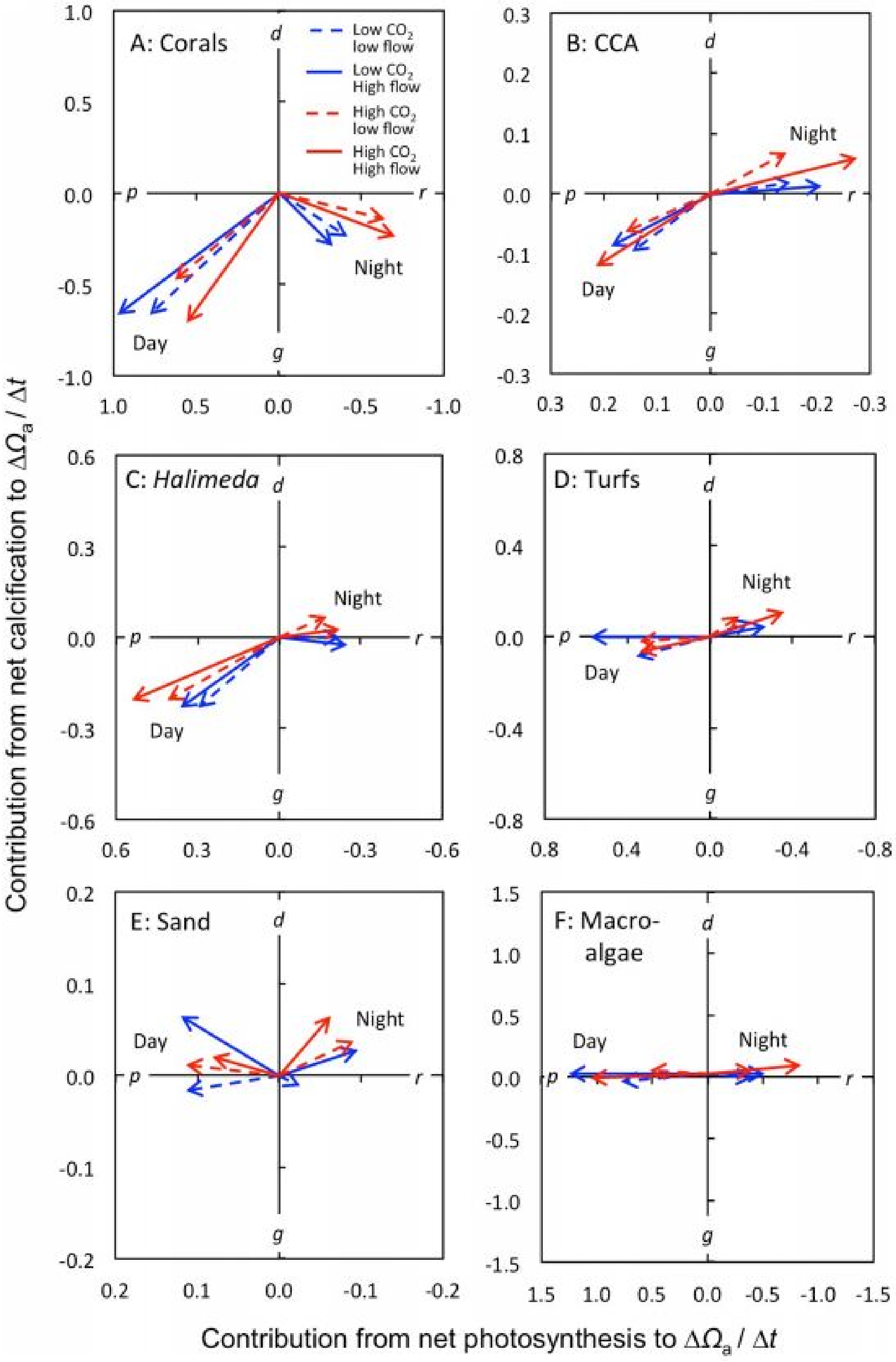

Figure 5.2 Contributions from net benthic photosynthesis and net benthic calcification to changes in aragonite saturation per unit time in shallow reef water (1 m depth). Symbols p, r, g, and d represent photosynthesis, respiration, calcification, and $CaCO_3$ dissolution. SOURCE: Anthony et al., 2013.

The extent to which the local OA mitigation potential of either group of primary producers can be realized at scale depends on a number of regional and local factors. Most critically, does the per-area drawdown of CO_2 by the seagrass meadow or macroalgal bed match the required Ω_a increase on the coral reef after accounting for differences in the areas of primary producers and coral reef? If so, then local OA mitigation has the potential to work at any scale. OA mitigation can also potentially operate at the scale of meters by managing mixed coral-algal communities, for example in embayments or in areas with high seawater residence times.

Risks

Seagrass meadows are vulnerable to ocean warming and cyclones (Waycott et al., 2009) whereas macroalgae are generally more resilient (Diaz-Pulido et al., 2007). Furthermore, while seagrass meadows have high conservation value (Cullen-Unsworth and Unsworth, 2016), whereas macroalgae are generally a competitor and indicator of reef decline (Bruno et al., 2009; Hughes et al., 1999; McClanahan et al., 2002; Mumby et al., 2007). This represents a dilemma from a local OA management perspective: On the one hand, the use of seagrasses in local OA management would serve two conservation objectives, but their climate vulnerability could jeopardize long-term OA management plans. On the other hand, macroalgae are relatively climate-hardy and can generate economic benefits if harvested, but they represent a risk to coral reefs. This risk is likely to be exacerbated under ocean acidification because it boosts the competitive dominance of some macroalgae over corals (Diaz-Pulido et al., 2011). Additionally, unless macroalgae are removed from the system, they will lead to reacidification and renutrification when they decompose, and under crowded conditions can lead to night-time anoxia (Greg Rau, presentation to committee).

Limitations

The efficacy of seagrasses and macroalgae as a local OA management tool is foremost limited by geographic setting, reef type and oceanography (McLeod et al., 2013). A small oceanic reef flushed by strong ocean currents will have minimal capacity for local OA mitigation. Conversely, a coral reef in a shallow embayment where water has high residence time or a reef in a coastal zone near dense seagrass beds will have the greatest scope. A key regional or local factor co-determining OA management efficacy is water quality, for two reasons. First, the growth rate of macroalgae is nutrient (but not carbon) limited (e.g., Schaffelke and Klumpp, 1998). Therefore, the scope for local OA mitigation by means of macroalgal management is likely to be greatest in coastal, nutrient-rich coral reef waters. In reef systems such as the Great Barrier Reef, where inshore waters are influenced by land-use runoff, Ω_a is already suppressed relative to that of the open ocean (Mongin et al., 2016b; Uthicke et al., 2014). Second, coastal shallow-water environments are the primary habitat for seagrasses (Grech and Coles, 2010). Although macroalgae are a ubiquitous component of coral reefs (McCook, 1999), their local abundance is driven primarily by a combination of grazing pressure (Mumby and Steneck, 2008) and nutrient supply (Burkepile et al., 2013).

The modeling study by Mongin et al. (2016a) illustrates the local OA management challenge on offshore reefs using reef macroalgae. They used a spatiotemporal model of water transport patterns to identify locations and harvesting schedules for macroalgal farms that maximize local Ω_a increase on Heron Island Reef. They showed that an optimal spatial configuration of farms, seaweed density, and harvesting protocol would elevate Ω_a by 0.1 over a 24 km^2 reef area. While this result appears insignificant in the context of open-ocean OA projections exceeding one or two Ω_a units (Cao and Caldeira, 2008), it is important to note that Mongin et al. (2016a) used small hypothetical algal farms (1.9 km^2) to counteract OA in a much larger downstream area where calcification and respiration are driving Ω_a in the opposite direction. Because Heron Reef is under strong oceanic influence and has high abundance of herbivores, the expected capacity for OA mitigation in this setting using macroalgae would be close to zero, so results from Mongin et al. (2016a) show surprising efficacy.

Infrastructure

Introduction of seagrass meadows and macroalgal beds relies on infrastructure commonly used for restoration efforts, including laboratories for propagule cultivation, and boats and divers for field transplants. Use of rhizomes has been found to be more successful than seeds or seedlings for restoration of seagrasses, along with the use of weights or staples to keep them in place (Katwijk et al., 2016). Macroalgae can be planted along submerged ropes to control their placement (Chung et al., 2013).

6

Conclusion

Coral reefs sit at the interface of two powerful societal trends. On the one hand, coral reef ecosystems provide vast resources to human communities, resources that are increasingly needed as the human population grows. On the other hand, coral reef ecosystems are existentially threatened by increased human-driven stresses, particularly the extensive coral mortality from severe bleaching events caused by warming seas on top of local stressors such as sedimentation, pollution, invasive species, and overfishing. Continuing disease threats and concerns about increasingly acidifying waters compound the risk posed to coral reefs. The increased reliance by humans on an ecosystem increasingly at risk of collapse has led to a widespread call for interventions that might preserve the services provided by coral reefs into the future.

A growing body of research on coral ecology, molecular biology, and responses to stress has revealed the complex nature of corals and their associated microbiome (including symbiotic algal, prokaryotic, fungal, and viral components). Some of this knowledge is poised to provide practical interventions in the short-term, whereas other discoveries are poised to facilitate research that may later open the doors to additional interventions.

The committee reviewed the current literature on new approaches with the potential to increase the resilience and persistence of coral reefs as global environmental conditions deteriorate. Current approaches that focus on management of local stressors, while important to continue, are not adequate, nor are they particularly designed, to address these rapidly changing environmental conditions. Reduction and mitigation of carbon emissions will go a long way in reversing and preventing future coral reef losses. However, even with such reductions, committed warming from the current accumulation of greenhouse gases is expected to expose the majority of the world’s reefs to harmful thermal stress events annually by 2050. Global bleaching events are already occurring due to the sensitivity of coral reefs to even small, sustained increases in maximum temperatures (as low as 1˚C). Thus, interventions that increase the persistence and resilience of coral reefs to current and deteriorating environmental scenarios are important to explore.

The constellation of interventions includes working with corals at a variety of ecological levels with a variety of tools. These levels include individual corals, their algal symbionts, microbial communities, populations within species, species, reef communities, and the associated gene repertoire at all these levels. Tools include movement of coral colonies, increasing populations through fragmentation or culturing, increasing natural resilience through artificial selection or selective breeding of corals and symbionts, preservation of coral stem cells or gametes, genetic intervention through gene editing in corals and symbionts, manipulation of microbial communities, and physical intervention to reduce stress. Table 6.1 provides an overview of the interventions as categorized by the committee.

TABLE 6.1 Overview of Interventions Examined in this Report

Intervention	What It Is	Current Feasibility	Potential Scale	Limitations	Risks
Genetic and Reproductive Interventions					
Managed Selection	Creating increased frequency of existing tolerance genes	Yes 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 lab 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 lab 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

The interventions range widely in their state of readiness. The committee explored these varied interventions and their potential for broad-scale implementation based on their benefits and goals, risks, scale of impact, limitations, and infrastructure needs. Layered over this discussion is that the risk of doing nothing is increasing quickly and is shown to be high in some reef environments experiencing significant losses.

GUIDING THEMES

Identifying versus Creating Resilience

Corals currently show a wide range of tolerance for heat and other types of environmental stresses, can inhabit a strong mosaic of environments, and can be associated with a diverse array of symbionts and microbes. This variability across populations of a species represents capacity for adaptation via natural selection. For instance, corals living in warm water microclimates are already adapted or acclimated to these conditions. A strong component of increasing the adaptive capacity of coral reefs is to map these adaptations, understand their function in the holobiont, and use them as potential targets for further genetic manipulation. Finding natural adaptive capacity for heat tolerance, and using it in programs of fragment outplanting or managed breeding represents a feasible, scalable approach that can potentially be undertaken in the near term on multiple species (see a similar conclusion in van Oppen et al., 2015a). Similar tools are well known in other fields, such as salmon and shellfish restoration. Interventions that focus on augmenting such natural resilience may have minimal barriers to implementation (e.g., permitting). While not risk free, if such tolerant variants can be found locally for multiple species, then there are fewer risks than, for example, genomic manipulation or long-distance relocation. However, it is not certain that natural levels of stress resistance, even for selectively bred and selected lines, will prove adequate to protect corals across the extreme conditions that might occur with future climate changes. To withstand unprecedented heat levels, it may be necessary to generate unprecedented genetic changes. Genomic manipulation of corals or symbionts is in very early research stages and faces a number of research hurdles before it is likely to be operational. Even when the technology is available for genetic transformation, it is currently unknown which genes are the best targets for alteration. Instead, there are a wide variety of potential targets in different corals that will need to be experimentally tested. Thus, the development of gene manipulation technology in corals and symbionts is simultaneously a tool for hypothesis testing about the most efficient gene targets, and a tool for generating manipulated genomes for use on reefs.

Novel Communities

A key feature of any intervention scheme for coral reefs is the movement of coral colonies to areas where they are needed to support reef stability. Whether new adaptive capacity is found on native reefs or generated in the laboratory, the most tolerant corals are likely to be a subset of the population with the expectation that this tolerance is heritable and will spread. Supporting the spread of tolerant types can take several forms. First, promoting propagation and breeding can support local stress-resistant populations so that their offspring can seed other reefs. Second, moving stress-tolerant colonies to adjacent reefs can help them pass their heat tolerance to future offspring in a wider location. Third, long-distance movement of tolerant corals from laboratories or warm water regions can potentially build thermal resistance in new or depleted areas. Short-distance relocation techniques are well known, and take advantage of decades of effort in coral colony nurseries. No known long-distance introductions of corals have been done purposefully. Marine research centers, extensive restoration programs, and the aquarium trade have already driven the developed techniques for outcropping and relocation over virtually any geographic scale. Movement of local stress-resistant colonies over short distances likely has the fewest risks and costs, and has the best potential to scale up. Movement of laboratory-generated colonies and movement across large distances have higher risks and costs.

The Value of Diversity

Coral reef ecosystems are built on diversity at the habitat, species, genetic, symbiont, and microbial levels. Large, diverse populations have a higher capacity for future adaptation and are likely to maintain abilities to respond to other stressors besides heat. Diversity also supports coral reef ecosystem function and the sustainable delivery of associated ecosystem services including fisheries and recreation. Interventions that focus on single species, genotypes, or symbionts may be important milestones in developing intervention technology and rescuing coral at these scales in the short term. However, sustaining coral reef ecosystems that will be exposed to a diversity of stressors will require multispecies approaches and consideration of the broad suite of both biological and ecological processes that underpin ecosystem resilience. This could potentially include the implementation of multiple interventions in one location.

Ecological Tradeoffs

Conceivably, all of the ecological and genetic interventions will change the diversity of a population or community. While these changes are intentional, they may come with unforeseen risks, particularly if they become uncontrolled. Even the use of seagrasses or macroalgae for mitigating ocean acidity may displace other corals and change the carbon and nutrient balance of the local system. Managed relocation of corals outside of their current range may cause corals to become invasive or move associated species that may overwhelm resident populations. Additionally, relocation of corals may inadvertently spread diseases. Manipulation of the symbiotic algae and microbiome similarly alters the diversity of the holobiont system. The microbiome impacts coral health in multiple ways that are not yet completely understood, and shifting the microbiome may have unintended consequences on health. A clear concern known from other fields is that the overuse of antibiotics, especially in open systems, can result in the emergence of unwanted antibiotic-resistant bacteria. Important context is the fact that changing climate conditions will also likely result in the development of novel communities with altered phenotypes and species assemblages (Lurgi et al., 2012).

Interventions that target a particular resilient trait may result in tradeoffs. For example, symbionts that are naturally more thermotolerant, such as those in *Durusdinium* (formerly *Symbiodinium* clade D), impart greater thermal tolerance to their coral hosts but may result in slower coral growth rates, reduced reproductive output, and disease susceptibility. Additionally, reducing the diversity of genotypes through genetic interventions reduces the ability to adapt via natural selection to unforeseen future stresses. Multiple stressors are often associated with coral declines and the inability to respond to multiple stressors is a risk to reef persistence. Interventions that reduce the light incidence may reduce photosynthetic activity of coral and other nearby organisms such as seagrasses. Artificial upwelling of cool water may lead to both nutrient and CO_2 enrichment from deeper waters.

The Complex Holobiont

Corals and their algal symbionts are a unit that responds uniquely to stress depending on the coral and symbiont genomes. Alteration of symbiont communities is known to increase heat tolerance for some corals. Manipulating each of these poses very different barriers to implementation, different levels of permanence, and different needs for technology development. They also impose different risks. Parallel efforts in native gene discovery, physiological testing, genetic manipulation, and selective breeding will be important investments.

Microbial communities associated with corals are highly diverse complexes with a wide spectrum of functions that impact the health and potential heat tolerance of the coral holobiont. Understanding the role of this microbiome in the physiological response of corals to their surrounding environment is just beginning. Therefore, while methods exist for influencing the microbiome through, for example, probiotics or antibiotics, the lack of knowledge of the specific associations between coral and microbe species limits targeted use of microbial intervention tools.

Achieving Scale

The spatial and temporal scales upon which interventions must operate depend on conservations goals, usually related to maintaining a certain level of local diversity and/or ecosystem services. To date, most interventions have operated on experimental or local scales, impacting a limited number of individuals. Some have the potential to be produced and applied at reef scales, including atmospheric shading and application of probiotics, antibiotics, antioxidants, and nutritional supplementation. However, delivering these interventions with specificity, with reduced risk, and at the required scale still has significant knowledge barriers. Others rely on large-scale efforts, at least at first, to achieve results beyond the individual. This encompasses efforts that require relocation or managed breeding in the laboratory and outplanting.

On the temporal scale, the effect of an intervention may be either permanent or self-perpetuating across generations, or it may be temporary, requiring either continuous or periodic reapplication during times of stress. Genetic interventions are intended to perpetuate themselves to future generations (unless they are limited to an epigenetic response), though it is likely that a degree of captive breeding and release could continue to be necessary. Physiological interventions affecting individual coral holobionts are generally not permanent and are unlikely to convey resilience to future generations. Managed relocation of coral individuals, if successful, has the potential to remain permanent. However, without eventual greenhouse gas mitigation (or other such reduction in the relevant stressor), continued change might drive the need for continued intervention.

Engineering the Local Environment

Although increase in average long-term ocean temperatures chronically stresses corals, bleaching events result in acute impacts that are concentrated in the summer period of weeks or months. These acute reactions to historically abnormally high temperatures might be reduced by transient, local manipulation of the heat or light environment. Furthermore, increasing acidity may be become a chronic and significant impact on corals in the future. Potential engineering solutions to these problems are being explored, but none are ready to be deployed on anything but an experimental scale. Additionally, the spatial scale at which they will ultimately have impact is a lingering question. Nevertheless, the ability to deploy this type of transient protection in the future may be important to protect high-value, live reef environments on local scales.

CONSIDERATIONS FOR IMPLEMENTATION

The task for this report is to synthesize current knowledge and lay the groundwork for informed decisions about conserving coral reefs under climate change. These decisions range from building investments in research programs and human capacity (i.e., researchers, practitioners) to deploying the interventions at experiment scales or integrated into restoration and conservation programs. Implementation of interventions in the ocean is regulated by permitting by multiple local, state, and national agencies for collection or outplanting of corals or for infrastructure installation. Overlapping responsibilities among resource agencies can lead to applications taking from months to years to pass all present regulatory requirements. Unknown risks from novel approaches may further complicate and delay permitting decisions, although permitting requirements are also a mechanism for establishing best management practices to mitigate risk through standardized and informed implementation. Due to the urgency of initiating responses to growing coral reef losses, identification of management and policy challenges is an important consideration along with scientific and technical challenges.

Adaptive Management

The interventions discussed in this report have not been implemented beyond experimental scales in the ocean, if at all, making their efficacy and impacts uncertain. Adaptive management is thus important for assessing the readiness of interventions for implementation at meaningful scales and their ability to meet conservation goals. An adaptive management approach can help account for and resolve key uncertainties in management practices with uncertain results, such as the approaches described in this report (Holling, 1978; Walters, 1986; Walters and Holling, 1990). The first stage of the adaptive management cycle is planning, based on existing best practices rooted in available science as well as predictive models, which can range from conceptual to statistical to mathematical, that generate expected outcomes for prioritizing management options and managing potential risks. The second stage of the adaptive management cycle is then doing, i.e., implementing a management action or suite of actions, with monitoring to evaluate management efficacy. The third stage of the adaptive management cycle is learning through the comparison of monitoring data to model predictions, which allows identification of knowledge and management gaps. The subsequent management adjustment restarts the adaptive management cycle to continually improve management through time. This adaptive management process can take one of two forms: (1) "passive adaptive management" of trying one best-expected management option at a time, or (2) "active adaptive management" of trying multiple alternative approaches that might have analogous expectations as experiments. Active adaptive management controls for confounding environmental variability and therefore enhances learning and the long-term outcome, at a potential cost to short-term performance.

Effective monitoring in adaptive management requires clear objectives and careful scientific design (Legg and Nagy, 2006). In monitoring for reintroduction projects such as coral reef restoration, a sequence of success metrics, from survival to reproductive success to population growth, can provide near-term feedback and directly measure achievement of long-term goals (Seddon, 1999). While the interventions described in this report share the long-term goal of increased coral persistence and resilience, the near-term monitoring metrics will inevitably vary by intervention. For example, temperature and its variability provide an immediate and easy-to-measure near-term metric of success for environmental interventions such as shading and mixing of cooling water. For genetic and physiological interventions such as managed selection, managed breeding, pre-exposure, and algal symbiont manipulation. “Omic” (genomic, transcriptomic, or proteomic) data could provide immediate and direct feedback on the increase in stress-tolerant genes or gene expression. Proteomics and transcriptomics can also provide near-term metrics of whether environmental interventions are successful at reducing stress on a level meaningful to coral gene expression and physiology. For any intervention involving coral gardening and outplanting, coral establishment, and growth serve as key near-term metrics of success. In the longer term, monitoring of community- and ecosystem-level metrics such as species diversity, persistence of key functional groups, and resilience to disturbance (SER, 2002), can inform achievement of the goal of maintaining functional coral reef ecosystems.

Monitoring potential drivers of failure (e.g., local stressors and conditions such as herbivore population sizes and sedimentation and pollution loads) is also necessary to engage in adaptive management (Armstrong and Seddon, 2007). While such drivers will factor into the “planning” stage as part of best practices for intervention approaches, given the inevitable variation in such factors between locations and through time, including them in the monitoring and “learning” stage as well will provide additional information for continued improvement of such best practices. For risky interventions such as many of those described here, monitoring of risk indicators (e.g., potential invasive species and diseases for managed relocation) can inform when to cease an intervention (if possible) to reduce the likelihood of unintended consequences.

Benefits, Risk, and Decision-Making

Assessment of the state of research on novel approaches alone does not provide the information needed to make decisions about implementing these approaches at large scales in the open ocean. The interventions described in this report have varying degrees and likelihoods of benefits and risks. They alter the environment with consequences that cannot completely be foreseen given the state of knowledge. While adaptive management provides a structured way of improving understanding of these benefits and risks, even this cannot be implemented without the decision to deploy these interventions in the ocean at least at an experimental scale. The presence of risk is not itself a barrier to action when evaluated in the context of the benefits they will confer. Additionally, comparison of these expected risks and benefits to the more traditional interventions (e.g., pollution reduction or marine protected areas) and to the risk of doing nothing is an important consideration, and one that will be dependent on the state of the environment and predicted risks to coral persistence.

The remainder of the committee's task, to be documented in a subsequent report, is to provide a framework for evaluating the relative risks and benefits of implementing these interventions. Additionally, the committee will develop a decision pathway to guide movement of these interventions from the research phase to implementation, when and where appropriate. Such a framework can be used to identify intervention strategies for which the consequences and costs may be justified. While it is not the committee's task to consider the social, policy, legal, and ethical considerations of implementing these approaches, these will be important to decision-makers as well.

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Glossary

Acclimation: The process of an individual organism adjusting to its environment

Adaptation via Natural Selection: Where organisms that possess heritable traits that enable them to better survive in their environment compared with other members of their species will be more likely to survive, reproduce, and pass more of their genes on to the next generation

Adaptive Gene Expression: Acclimatory changes to gene expression due to changes in the frequencies of gene regulatory variants or other DNA-based controls of gene expression

Aerosols: Particles suspended in air

Alkalinity: The capacity of water to buffer changes in pH, frequently occurring through the presence of calcium carbonate

Allee Effect: Reduced fitness caused by a low population density

Allele: A variant form of a gene at a particular locus on a chromosome

Aragonite: A form of calcium carbonate used by marine calcifiers (e.g., coral) to build skeletons

Aragonite Saturation State (Ω_a): The concentration of aragonite ions in seawater, influencing the ability for marine calcifiers to build their skeletons

Bleaching: A response by corals to stress that includes the ejection of symbiotic algae, resulting in a loss of color

Broodstock: Individuals held in facilities for breeding

Calcium Carbonate ($CaCO_3$): A biologically important mineral found in rocks and dissolved in seawater used by calcifying organisms to build skeletons

Colony (coral): A group of genetically identical coral polyps

Community: The individuals of all species within a defined ecological area

Coral Gardening: The propagation of coral fragments in nurseries

Cultivation: Rearing of organisms in a controlled environment such as a nursery or laboratory

CRISPR/Cas9: A gene editing platform in which an endonuclease and a guide RNA are used to introduce double strand breaks at a specified location within the genome

Degree Heating Week: A coral bleaching susceptibility metric defined by the sum of excess degrees of heat over the number of weeks of exposure

Dinoflagellates: Single-celled algae from the phylum Dinoflagellata, including those symbiotic to coral

Dysbiosis: Disruption in the balance of a body's microbiota

Epigenetic: Modifications to DNA that are not sequence-based but control gene expression

Fragmentation: Division of a coral colony into genetically identical pieces

Gamete: The sperm and eggs cells that fuse for fertilization

Gene: A segment of DNA that serves as the basic unit of heredity

Gene Drive: A system of biased inheritance in which the ability of a genetic element to pass from a parent to its offspring through sexual reproduction is enhanced

Gene Flow: The transfer of genetic information from one population into another population

Genetic Rescue: An increase in population fitness due to the introduction of new alleles

Genome: The complete sequence of DNA in an organism

Genotype: The traits of an organism defined by its genome

Heterosis: Increased fitness in offspring compared to the parents

Hormesis: Where a beneficial response is induced following the application of a low dose of a stressor that would be harmful at higher doses

Hybrid: The offspring of two plants or animals of different species or varieties

Macroalgae: Multicellular algae, frequently known as seaweed

Metabolomics: The study of metabolites—molecules used in metabolism

Microbiome: Microorganisms within a defined community including prokaryotes, fungi, viruses, and algae

Ocean Acidification: Reduction in the pH of the ocean caused by increasing concentration of CO_2

Ontogeny: The development of an organism from the time of fertilization to the adult form

Outbreeding Depression: A result of outcrossing where there is a loss of local adaptation or disruption of co-adapted gene complexes that lead to a reduction in fitness

Outcrossing: Breeding of individuals that are not closely related to introduce genetic diversity

Phage: Viruses that specifically target and infect bacteria

Phenotype: The observable traits of an organism

Photo-oxidation: Chemical breakdown in the presence of oxygen caused by light

Physiological: Pertaining to an organism's body parts and functions

Planula: A free-swimming larva characterized by a flattened, ciliated shape

Polyp (coral): The form of an individual coral animal and other Cnidarians such as sea anemones

Population: All of the individuals of a given species within a defined ecological area

Propagule: Any form of an animal that acts as the basis for transmission to new areas

Proteomics: The study of proteins

Reactive Oxygen Species: Oxygenated molecules whose productive is increased in times of stress and may cause damage cells

Representative Concentration Pathway (RCP): Scenarios of future greenhouse gas concentration trajectories based on possible emissions and response options, developed by the Intergovernmental Panel on Climate Change

Scleractinia: The taxonomic order of hard skeleton, reef-building corals

Selection: Differential survival and reproduction of organisms

Symbiodiniaceae: The taxonomic family of dinoflagellates symbiotic to coral

Symbiont: An organism living symbiotically with another, either as an endosymbiont (within the host's cells) or an exosymbiont (outside of the host's cells)

Transcriptomics: The study of transcriptomes, the RNA molecules in a cell

Unfolded Protein Response: A cellular response to the protein unfolding which can occur as a result of environmental stress

Xanthophyll Cycling: A mechanisms in algae and plants for dissipating energy caused by light incidence to protect photosynthetic reaction centers

Zooxanthellae: Single-celled photosynthetic dinoflagellates that live symbiotically with marine organisms, including coral

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 lab 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 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 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 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 lab 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 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

B.A. from the University of California, Berkeley in Molecular & Cell Biology and Integrative Biology, and she received her Ph.D. 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. EPA 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

Susan Roberts became the director of the Ocean Studies Board in April 2004. Dr. Roberts received her Ph.D. in marine biology from the Scripps Institution of Oceanography. Prior to her position at the Ocean Studies Board, she worked as a postdoctoral researcher at the University of California, Berkeley and as a senior staff fellow at the National Institutes of Health. Dr. Roberts' research experience has included fish physiology and biochemistry, marine bacterial symbioses, developmental cell biology, and environmentally induced leukemia. Dr. Roberts specializes in the science and management of living marine resources. She has served as study director for reports produced by the National Research Council on topics covering a broad range of ocean science, marine resource management, and science policy issues. She is a member of the U.S. National Committee for the Intergovernmental Oceanographic Commission (IOC) and serves on the IOC panel for the Global Ocean Science Report. Dr. Roberts is a member of AAAS, American Geophysical Union, and the Association for the Sciences of Limnology and Oceanography. She is an elected Fellow of the Washington Academy of Sciences.

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 B.A. 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
Information Gathering Meeting Agendas

INTERVENTIONS TO INCREASE THE RESILIENCE OF CORAL REEFS WORKSHOP 1 AGENDA

May 31, 2018

University of Miami Rosenstiel School of Marine and Atmospheric Science
4600 Rickenbacker Causeway | Miami, FL 33149
Marine Science Center Auditorium

Workshop Goal: Discussions at the workshop will explore the state of the science, the risks, and the benefits of ecological and genetic interventions with the potential to increase the long-term persistence of coral reefs in environmentally degraded scenarios. The workshop is one component of the information-gathering activities that may inform the deliberations of the National Academies' Committee on Interventions to Increase the Resilience of Coral Reefs. Additional public information-gathering activities will be conducted.

8:00 AM *Breakfast*

8:30 AM **Introduction**
Stephen Palumbi, *Committee Chair*

8:45 AM **Opportunities and challenges for coral restoration in the Caribbean--perspectives from science and management**

- What are the current and expected future conditions in the Caribbean and the expected effect on coral reefs? What are the uncertainties in predicting the condition of coral reefs in the future?
- What information is needed to weigh the risk and benefit of implementing new coral reef restoration and management approaches?
- What are the regulatory and scientific needs for permitting research and deployment of new approaches in the water?

Derek Manzello, *NOAA's Atlantic Oceanographic & Meteorological Laboratory*
Erinn Muller, *Mote Marine Laboratory*

Reef Management Panel:
Sarah Fangman, *Florida Keys National Marine Sanctuary*
Lisa Gregg, *Florida Fish and Wildlife Conservation Commission*

Ernesto Díaz, *Puerto Rico Coastal Zone Management Program*

10:45 AM *Break*

11:00 AM **Restoring coral reefs through artificial propagation and enhancing sexual recruitment**

- What are the challenges for restoring coral reefs and how are they addressed through artificial propagation and recruitment? What gaps remain?
- What are appropriate metrics of success to evaluate restoration success in a stressed and changing environment?
- How can restoration practices be integrated with ecological and genetic interventions implemented in the wild? What scale can be targeted?

Diego Lirman, *University of Miami*
Margaret Miller, *SECORE*

12:00 PM *Lunch*

1:00 PM **The genomic basis for coral adaptability and resilience**

- What is known about the genetic (genome to population scale) considerations and risks for artificial selection of resilient coral?
- What is the possibility of manipulating the coral genome to improve resilience? What advancements are needed to achieve this at scale?

Iliana Baums, *Pennsylvania State University* (remote)
Manuel Aranda, *King Abdullah University of Science & Technology* (remote)
Phil Cleves, *Stanford University*
Mikhail Matz, *University of Texas Austin*

2:40 PM *Break*

2:50 PM **Manipulating the coral-algal symbiont**

- What is the specificity of algal symbionts to host coral? How does this influence holobiont resilience?
- What is known about the feasibility and risk (e.g., failure, ecological changes) to manipulating symbiotic relationships? Can this be done at scale?

Todd LaJeunesse, *Pennsylvania State University*
Ross Cunning, *University of Miami*
Hollie Putnam, *University of Rhode Island* (remote)
Kate Quigley, *Australian Institute of Marine Science* (remote)

4:30 PM **The coral microbiome influence on coral resilience**

- What is known about the influence of the microbiome on coral (e.g., health, adaptability, reproduction, energetics)?

- What is the feasibility and potential benefit of applying a probiotic approach to managing resilience? Can this be done at scale?

Rebecca Vega Thurber, *Oregon State University* (remote)
Raquel Peixoto, *Federal University of Rio de Janeiro*

5:30 PM *Adjourn*

INTERVENTIONS TO INCREASE THE RESILIENCE OF CORAL REEFS

WEBINAR: ENVIRONMENTAL INTERVENTIONS TO PROMOTE CORAL REEF PERSISTENCE

4:00- 5:30 ET
August 2, 2018

Webinar Goal: The presentations and discussions on the webinar will explore the state of the science, the risks, and the benefits of environmental interventions with the potential to increase the long-term persistence of coral reefs in environmentally degraded scenarios. This webinar will touch on questions, such as:

- Does the intervention return the environment to pre-stressed conditions? Is that change temporary or long term?
- What scale does the intervention need to be applied to change conditions?
- What are the technical barriers/considerations surrounding this intervention?
- What are the potential unintended consequences?

The webinar is one component of the information-gathering activities that may inform the deliberations of the National Academies' Committee on Interventions to Increase the Resilience of Coral Reefs.

4:00 PM **Opening Remarks:** Ken Anthony, *Committee Member*

4:05 PM **Context on Future Conditions:** Mark Eakin, *NOAA*

4:15 PM **Interventions to Address Ocean Acidification: G**reg Rau, *University of California Santa Cruz*

4:40 PM **Shading and Cooling Interventions:** Mark Baird, *CSIRO*

5:05 PM **Marine Cloud Brightening:** Robert Wood, *University of Washington*

5:30 PM **Adjourn**

INTERVENTIONS TO INCREASE THE RESILIENCE OF CORAL REEFS
WORKSHOP 2 AGENDA

August 28, 2018

East-West Center's Hawaii Imin International Conference Center
1777 East-West Road, Honolulu, Hawaii 96848 (on University of Hawaii Manoa campus)
Asia Room

Workshop Goal: Discussions at the workshop will explore ways of evaluating the risks and benefits of ecological, genetic, and environmental interventions with the potential to increase the long-term persistence of coral reefs in environmentally degraded scenarios. The workshop is one component of the information-gathering activities that may inform the deliberations of the National Academies' Committee on Interventions to Increase the Resilience of Coral Reefs.

8:00 AM *Breakfast*

8:30 AM **Introduction**
Stephen Palumbi, *Committee Chair*

8:45 AM **Opportunities and challenges for coral restoration in the Pacific--perspectives from science and management**

- What are the current and expected future conditions in the Pacific and the expected effect on coral reefs? What are the uncertainties in predicting the condition of coral reefs in the future?
- What information is needed to weigh the risk and benefit of implementing new coral reef restoration and management approaches?
- What are the regulatory and scientific barriers and needs for permitting research and deployment of new approaches in the water?

Russell Sparks, *Hawaii Division of Aquatic Resources*
Gerry Davis, *National Oceanic and Atmospheric Administration*
Lance Smith, *National Oceanic and Atmospheric Administration*
Fran Castro, *University of Guam*
Dave Wachenfeld, *Great Barrier Reef Marine Park Authority (remote)*

10:30 AM *Break*

10:45 AM **Reef Restoration and Adaptation Program**

Line Bay, *Australian Institute of Marine Science*

11:45 AM **Benefits and risks of interventions to increase thermal tolerance**

Madeleine van Oppen, *Australian Institute of Marine Science and University of Melbourne (remote)*

12:30 PM *Lunch*

1:30 PM **Risks from invasion and disease introduction**

- Under what conditions have invasive species and disease been introduced and intensified in coral reefs? What is the ability to predict the probability of these introductions?
- How may deteriorating environmental conditions, as well as manipulation of a reef community, affect susceptibility to invasive species and disease?
- How may translocation of coral and associated reef species to new areas lead to spread of known invasive and disease, or cause coral themselves to become invasive?

Celia Smith, *University of Hawaii at Manoa*
Joleah Lamb, *Cornell University*
Drew Harvell, *Cornell University (remote)*

2:45 PM **The risk of doing nothing: the value of coral reefs and active intervention**

- Which ecosystem structures and functions are imperative to preserve to maintain coral reefs? How will deteriorating environmental conditions inhibit their maintenance?
- Which ecosystem structures and functions may change when moving toward resilient reefs? How do we evaluate the risks introduced by interventions that alter coral reefs communities?

Kirsten Oleson, *University of Hawaii at Manoa*

3:15 PM *Break*

3:30 PM **Frameworks for evaluating interventions: lessons from other taxa**

3:30 PM Invasion Ecology: Jeb Byers, *University of Georgia (remote)*

4:00 PM Managed Breeding: Robin Waples, *National Oceanic and Atmospheric Administration (remote)*

4:30 PM Managing Disease: Jared Westbrook, *American Chestnut Foundation*

5:00 PM Structured Decision Making and Adaptive Management: Michael Runge, *U.S. Geological Survey*

5:30 PM *Adjourn*