

BUILDING LONG-TERM REEF RESILIENCE

CHAPTER 3

3. BUILDING LONG-TERM REEF RESILIENCE

There is widespread agreement that increasing coastal populations and projected increases in sea temperatures will continue to increase pressures to coral reefs, and that the need for effective coral reef management has never been greater^{9, 11, 13, 23, 28, 31, 42, 47}. Management efforts that increase reef resilience will play a critical role in determining the future of coral reefs by allowing species to adapt and adjust before irreversible damage occurs⁷⁵. The concept of resilience is based on well-established scientific principles, and its use in strategic management of coral reefs offers insights and approaches that are becoming increasingly critical for the protection of these complex ecosystems.

In the context of mass bleaching, resilience can be thought of as the integrated result of coral resistance to heat stress, coral survival during bleaching, and reef recovery after bleaching-related mortality (Section 3.1). Managers can take active steps toward restoring and maintaining the long-term resilience of coral reef ecosystems. Managers can support coral reef ecosystem resilience in two ways: (1) by incorporating existing resilient areas into management design; and (2) by implementing strategies to either reinstate or protect factors that confer resilience, such as good environmental conditions, biological diversity, and connectivity.

Incorporating resilient areas into spatial networks for reef management requires knowledge of the location of resilient reefs. There is an emerging knowledge of how to identify and classify these areas (Section 3.2).

Factors that confer resilience can be reinstated or protected using a range of conventional management strategies that focus on management of local stressors. MPAs can be used to manage direct threats to reefs, such as those that may result from fishing and recreation practices (Section 3.3). Broader management approaches, such as watershed management and integrated coastal management (ICM) can manage indirect threats to reefs, such as those resulting from coastal developments and agricultural land use (Section 3.4). In some cases, restoration measures may also be appropriate to increase overall resilience (Section 3.5). While there may already be management action directed at localised issues such as fishing, pollution and recreation, controls may need to become more conservative given predicted increases in the frequency of bleaching events⁹. This section explores ideas about coral reef resilience and the management actions that can build resilience in the context of mass coral bleaching.

Two ways of supporting coral reef ecosystem resilience are (1) by incorporating existing resilient areas into management design and (2) by implementing strategies to either reinstate or protect factors that confer resilience, such as good environmental conditions, biological diversity, and connectivity

3.1 Resilience

Coral reef ecosystems are highly dynamic systems that have evolved to cope with a wide range of disturbances. While a resilient system will have the best chance of coping with future threats, human influences have eroded the natural resilience of many coral reef systems, reducing their capacity to cope with disturbance. Strategies aimed at rebuilding and supporting the resilience of these systems are the best investment for ensuring that reefs can continue to provide the goods and services upon which humans depend^{11,76}. This section introduces the concept of resilience and describes the factors that confer resilience on coral reef ecosystems.

3.1.1 Defining resilience

Ecosystem resilience relates to the ability of the system to maintain key functions and processes in the face of stresses or pressures by either resisting or adapting to change^{76,77}. For coral reef ecosystems, resilience characterises the capacity to maintain the dominance of hard corals and/or to maintain morphological diversity, rather than shifting to a predominantly algal state or a single coral morphology. Resilience also includes the potential of the system to reorganise and build its capacity to adapt to change⁷⁸. As an example, a resilient coral community might suffer significant coral mortality from a bleaching event, but reorganise so that the community composition shifts toward different coral species that provide similar habitat and are more tolerant to coral bleaching.

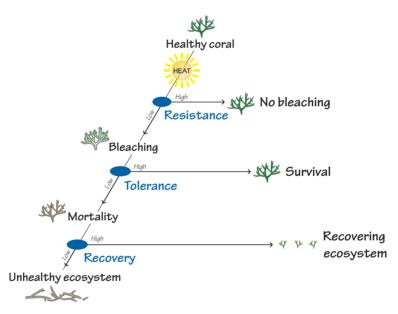


Figure 3.1 Coral reef ecosystem resilience to mass coral bleaching

Ecosystem resilience relates to the ability of the system to maintain key functions and processes in the face of stresses by either resisting or adapting to change. The resilience of coral reef ecosystems to mass coral bleaching can be thought of as the integrated result of coral 'resistance' to heat stress, coral 'tolerance' during bleaching events, and reef 'recovery' after bleaching-related coral mortality.'Resistance' determines the extent to which corals either withstand exposure to heat stress or bleach. Once bleached, tolerance determines the extent to which corals either survive the bleaching event or die. When coral mortality is high, reef recovery determines the extent to which the system either re-establishes coral dominance or remains degraded. Coral resistance, coral tolerance, and reef recovery are determined by a number of factors that can be broadly grouped into four categories: (1) ecosystem condition, (2) biological diversity, (3) connectivity between areas and (4) local environmental conditions. Implementing actions that either protect or strengthen these four resilience-conferring factors can help coral reef ecosystems survive predicted increases in the frequency and severity of mass coral bleaching events. Adapted from Obura (2005)⁸⁸.

In the context of mass bleaching, resilience can be considered as the capacity of the coral community to resist, survive, or recover after recurrent bleaching events (Figure 3.1). A resilient reef may suffer significant coral mortality during a bleaching event, but will maintain key system characteristics (structure and function) through rapid recovery and reorganisation, relative to less resilient reefs. The capacity of coral reefs to recover from disturbances will become increasingly important if the frequency and severity of bleaching events increases. Reefs with lowered resilience are more likely to suffer serious and long-lasting impacts from coral bleaching events.

In a broader context, the cumulative effects of global and local stressors will determine the long-term resilience of coral reef ecosystems. While both global and local stressors can support or degrade the factors that confer resilience on reef ecosystems, local stressors are much easier to manage in the short term. These resilience factors are discussed below. Implications for the management of local stressors are discussed in Sections 3.3 and 3.4.

3.1.2 Factors that confer resilience

Factors that influence the resilience of coral reef ecosystems can be grouped into four categories: (1) ecosystem condition, (2) biological diversity, (3) connectivity and (4) local environment. Each of these categories includes attributes that can strengthen resistance, survival, and recovery from mass bleaching as well as recovery from other types of disturbances.

Ecosystem condition. Ecosystem condition includes coral condition, coral cover, water quality, and fish abundance. These attributes influence survivorship during mass bleaching events and recovery after mass bleaching events or other disturbances. Corals that are stressed or in poor condition, as indicated by low lipid levels, suppressed immunity, or high levels of stress metabolites, may be less likely to survive the stresses associated with coral bleaching⁴¹. Coral cover, water quality, and fish abundance are critical factors determining reef recovery through their influence on a range of processes including: larval supply, availability of substrate for settlement, coral recruitment rates and survivorship of juvenile corals (see Section 4.2.3). Management efforts that effectively strengthen ecosystem condition are likely to play a major role in facilitating recovery processes in reefs affected by climate change⁴⁷.

Coral condition, amount of coral cover, water quality, and fish abundance are attributes of ecosystem condition that are likely to play a major role in determining coral reef ecosystem resilience to climate change *Biological diversity.* Biological diversity plays an important role in determining resilience, especially through the influence of genetic diversity within species and species diversity within ecosystem functions. These attributes influence coral resistance to bleaching, coral survivorship during bleaching, and reef recovery after mass bleaching mortalities or mortalities from other disturbances. In particular, genetic variation in zooxanthellae may play a role in influencing resistance to

mass bleaching⁷⁹. Genetic differences between corals also strongly influence the outcome of bleaching events, with coral type being a major determinant of a coral's susceptibility to bleaching and the rate at which it can recover from bleaching⁸⁰.

The importance of these sources of diversity becomes increasingly significant over time as reef ecosystems are repeatedly exposed to thermal stresses. When a diversity of species fulfils a function (for example branching corals providing habitat for small fish), the loss of a single species will not lead to loss of the function. This functional redundancy is a key characteristic of resilient systems⁸¹. Biological diversity also plays a practical function in protecting ecosystems from future threats through maximising the diversity of responses¹¹. A system is less prone to collapse when key functions are performed by multiple species that respond differently to stress or disturbance events. Like functional redundancy, response diversity minimises the chance that any one disturbance will eliminate all organisms performing a key function.

The importance of biological diversity in conferring resilience is well illustrated by the role of herbivores in coral reef ecosystems. In a case study from Jamaica⁸², overfishing had prevented herbivorous fishes from playing a significant role in controlling algal growth. At that point, the herbivory function, which works to ensure the availability of substrate suitable for new coral recruits, was dependent on the sea urchin, *Diadema*

Biological diversity confers resilience because different species are likely to respond differently to stress and disturbance events, increasing the chance that some species will survive and continue to perform key ecceystem functions

antillarum. Subsequently, a disease epidemic killed most of the urchin population, leaving too few herbivores in the system to adequately remove algae. When a major storm caused widespread damage to coral communities, unchecked algal growth prevented substantial recovery of corals. These reefs have remained algal-dominated for decades. Overfishing and reduced functional redundancy made the system highly susceptible to disturbances and led to a phase shift towards an algal-dominated system with a substantially lower capacity to provide ecosystem services to humans. If a diversity of herbivores had been present and fishing pressures better managed, the system would have been protected through functional redundancy and less prone to collapse.

Connectivity. The capacity of a system to recover or reorganise following a disturbance is an important element in determining resilience. Connectivity plays a central role in determining this potential as it influences the likelihood that damaged reefs will be replenished by 'seed' reefs or refugia. In the context of resilience, it is

important to realise that connectivity is more than larvae drifting in largely unmanageable ocean currents. Much of the connectivity in reef ecosystems depends on intact and healthy non-reef habitats, such as inter-reef hard bottom communities or seagrass beds⁸³. These non-reef habitats are particularly important to the maintenance and regeneration of populations. They will become increasingly critical as reef systems spend greater time in recovery mode due to severe and more frequent disturbance events, such as temperature-related coral bleaching. Management efforts that provide effective protection for each of the critical habitat types will play a key role in restoring and maintaining the capacity of the coral reef system to adapt to increased frequency and severity of mass coral bleaching.

Connectivity plays a central role in determining coral reef ecosystem resilience as it influences the likelihood that damaged reefs will be replenished by 'seed' reefs or refugia.

BUILDING RESILIENCE

Variation in the local environment can determine coral reef exposure to heat stress, light levels, or current speed – all factors that influence coral reef resilience to bleaching *Local environment.* Variation in the local environment can determine exposure to heat stress, light levels, or current speed – factors that influence resistance and tolerance to bleaching. For example, exposure to heat stress will vary depending on location within the reef (such as reef flat compared to reef slope) or, at a larger

scale, a reef's orientation with respect to upwelling. In some situations, shading from cliffs or mountains along the shoreline can reduce light levels and decrease bleaching risk. In this context, topographic complexity can play an important role in determining the amount of variation in the local environment of corals. This further increases the imperative for reef managers to protect species diversity and thereby minimise the chances of reducing variation in the local environment. The role of local environmental factors in resilience makes it a useful feature for identifying resilient areas, as discussed in the next section.

3.2 Identifying resilient coral reef areas

Identifying coral reef areas that are resilient to mass coral bleaching and protecting these areas from localised stressors offers the potential to create a network of refugia that can replenish other areas that are more vulnerable to bleaching The severity of bleaching responses varies between reefs during mass bleaching events¹⁹¹¹⁸. Identification of areas that have historically had high resilience to bleaching provides the basis for a network of refugia to underpin resilience-based management of the reef ecosystem. Refugia serve as a seed bank to facilitate the recovery of areas with lower natural resilience, and will play a central role in networks of protected areas designed to maximise ecosystem resilience.

The identification of resilient areas as an ecosystem management strategy is already being applied in various locations around the world. Examples of resilience-based management initiatives include projects in Palau (A. Smith, pers. comm.), the British Virgin Islands (S. Wear, pers. comm.), Belize (S. Walsh and M. McField, pers. comm.), the Seychelles (J. Neville, pers. comm.), Yemen⁸⁴, and the Maldives (G. Dews, pers. comm.). The experiences gained from these initiatives will help to refine knowledge and develop additional protocols for the identification of resilient areas. The outcomes of these early tests of resilience management strategies will also provide important information about the extent to which the factors that confer resilience on an area will remain consistent over time.

The Nature Conservancy, together with a group of partners, has developed a *Reef Resilience* (R^2) *Toolkit* to help managers develop and apply resilience principles for managing coral reefs³⁹. This section draws from the R^2 toolkit to review the features that characterise resilient reefs (Section 3.2.1), and to outline how to identify areas of high resilience (Section 3.2.2). Managers are directed to the R^2 toolkit or website (www.reefresilience.org) for a more detailed discussion of how to identify resilient areas and incorporate these areas into MPA design.

3.2.1 Characteristics of resilient coral reef areas

Patterns of past bleaching responses, mortality and reef recovery provide insights into an area's resilience to mass coral bleaching events. Based on evidence from the literature and systematically compiled observations from researchers in the field, a number of factors that correlate with resilience to coral bleaching have been identified⁴⁰. Resilience to bleaching is associated with features that:

- Reduce sea temperature stress, eg localised upwelling, proximity to deep or cooler water
- Increase water movement in order to flush harmful toxins, eg topographic features such as narrow channels, strong currents
- Screen corals from damaging radiation, eg high island shading, reef shelf shading, aspect relative to the sun, or water turbidity
- Indicate potential pre-adaptation to temperature and other stressors, eg highly variable temperature regimes, regular exposure at low tides, history of corals surviving bleaching events
- Indicate strong recovery potential, eg abundance of coral larvae or strong recruitment
- Improve coral larval transport to the site, eg connectivity with source reefs
- Maintain a favourable substrate for coral larval recruitment, eg diverse community structure present, healthy and stable populations of herbivores.

3.2.2 How to identify resilient areas

There are two broad approaches to selecting reef areas that are likely to be resilient to mass coral bleaching: (1) identifying areas based on their response to past incidents of anomalous sea surface temperatures and (2) predicting areas based on the presence of characteristics expected to confer resilience.

Identifying resilient areas from past responses. The response of corals and reef communities during previous bleaching events can provide important pointers to sites that may be inherently resilient to coral bleaching. There is uncertainty about the extent to which past patterns will be repeated during future mass bleaching events, and data should be interpreted carefully. In addition, identifying sites that display a demonstrated resilience to bleaching requires reliable information about levels of heat stress during bleaching events, and knowledge about the extent of bleaching for sites of interest. Figure 3.2 (based on Done et al⁸⁵) provides a decision tree for identifying areas to target for management based on their resilience to past sea temperature anomalies.

A site's potential resilience is one of several factors that should guide decisions relating to the selection of areas for increased management. The first step in a management planning process is to identify candidate sites based on conventional criteria for site selection. The eligibility of sites for protection should be evaluated on the basis of social, economic, ecological, regional or pragmatic criteria⁹⁶. The criteria used should be carefully chosen so that the selection process meets the specific objectives of the planned management regime.

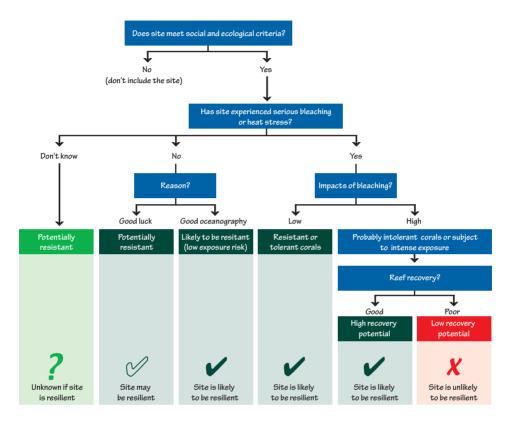


Figure 3.2 Decision tree for identifying resilient areas for increased management based on past responses to heat stress and bleaching (adapted from Done et al⁸⁵)

Coral reef community response during previous bleaching events can provide important pointers to sites that may be inherently resilient to coral bleaching. If a site warrants increased management protection based on conventional social and ecological selection criteria (see Salm et al⁸⁶ for further discussion about selection criteria), its potential resilience can be assessed by first evaluating its historical exposure to heat stress. A site that has not experienced previous exposure to stressful temperatures may be resilient to mass bleaching, depending on the reasons for its good luck. A site that has been exposed to stressful temperatures may still be resilient to mass bleaching if it has been tolerant to the bleaching event and exhibited high levels of coral survival. Finally, sites that suffered high coral mortality during past bleaching events may still be resilient if the site has demonstrated a good rate of recovery (years rather than decades).

At each of the candidate sites, heat exposure and past bleaching responses should be evaluated. Sites should initially be divided into those that have experienced serious bleaching or heat stress previously, and those that have not. Current information about thermal stress, presented as sea surface temperature anomalies, is now readily accessible to most reef managers through the NOAA HotSpot program, freely available on the Internet (see Section 2.2.2). HotSpot maps ($50 \times 50 \text{ km}$) visualise differences in exposure to thermal stress at a larger spatial scale. This can be readily supplemented with reef-scale measurements obtained from direct temperature readings with thermometers or inexpensive data loggers. Local bleaching thresholds can then be refined by maintaining temperature records and correlating measures of thermal stress with observed bleaching responses.

It is revealing to examine possible reasons for some reefs having no recorded history of anomalously high water temperatures. If sites have low risk of exposure to high water temperatures because of their oceanography or other physical characteristics, they may prove to be resistant to bleaching in the future. In examining the reasons for low exposure, it may be useful to question whether the feature conferring resilience in the past is likely to remain unchanged in the future. For example, shading from cliffs is unlikely to change but currents may shift under various climate scenarios. However, in many cases it may not be possible to identify the mechanisms or characteristics that have resulted in a site being spared exposure to heat stress. In other cases, it may not be possible to ascertain whether a site previously experienced heat stress. In both of these situations, the resilience of the reef community to bleaching has to be assessed using other criteria, such as community composition and recovery rates following recent disturbances. Managers should consider implementing a monitoring program at these sites to document their response to any future episodes of thermal stress.

The next step is to examine the response of reefs that are known to have experienced thermal stress in the past. Reefs that have suffered only minor coral mortality during previous anomalies are likely to be populated by corals that are resistant to bleaching, or that have a high tolerance for bleaching. These reefs are probably sites of high resilience, unless they were only exposed to minor stress. If the latter is the true case, then it is difficult to predict whether they are likely to be resistant or tolerant to more extreme temperature stresses in the future.

Determining the thermal history of reef sites can be difficult, especially if managers do not have access to historical satellite-derived or in situ temperature data. However, even in remote locations there may be long-term temperature monitoring programs being run by researchers or other organisations (such as meteorological or shipping agencies). Local knowledge should also be sought and collated, as some regular reef users, such as tourism operators and fishers, have an intimate, longer-term perspective about the conditions on their reefs that can help deduce the occurrence of anomalies.

The remaining category of sites includes those that have suffered substantial mortality following exposure to stressful temperatures. The rate of recovery at these sites provides important information about their resilience. Damaged sites that show high rates of recovery are resilient. Sites with low rates of recovery are not resilient, unless the causes of slow recovery can be identified and remedied by management action.

Predicting areas of resilience. In many instances, it may not be possible to assess the response of reef sites to thermal stress. This may be because bleaching has not occurred in the past, or because there is not sufficient information about either the exposure of different sites to high sea temperatures or its effect on reef organisms. In these cases, reef managers may still be able to include bleaching resilience in their management plans by identifying areas that are characterised by factors that are known to contribute to resilience.

Section 3.2.1 outlines a set of key characteristics that have been identified from observations of the characteristics of reefs that have proven resilient to past bleaching events, or have been derived from general principles of coral community dynamics. The R² Toolkit provides detailed guidance and data sources for gathering information about these characteristics. Table 3.1, adapted from R², summarises information sources that can be used to assess these characteristics and, thus, predict site resilience to mass bleaching. The role of these characteristics in conferring resilience to mass coral bleaching events is explored below.

The R² Toolkit identifies five characteristics thought to confer resilience to mass coral bleaching: cool water, shading, screening, resistant coral communities, and high recovery rates I. Cool water. Some sites may have consistently cooler water due to upwelling or proximity to deep water. Local bathymetry, regional and local currents and prevailing winds may all play an important role in reducing the temperature of water bathing a reef. Case study 6 describes research that is developing hydrodynamic models of Palau to predict future sea

temperatures in order to identify areas that may be protected from mass bleaching by cooler waters. Some researchers have suggested that currents may not be a reliable source of long-term resilience because climate change may result in new current patterns⁸⁷.

2. Shading. Some reefs may also be protected from bleaching stress by shading where sun exposure is limited by topographic or bathymetric features. Reefs shaded by cliffs or mountainous shorelines may be at reduced risk of bleaching. While many reef areas are unlikely to be associated with features that can provide shade, fringing reef complexes around steep-sided limestone or volcanic islands, such as occurs in Palau and the Philippines, may have many shaded sites.

3. Screening. Unnatural levels of sediments and excessive phytoplankton growth from nutrient-enrichment can stress and kill corals. However, naturally turbid conditions may filter or screen sunlight, providing a measure of protection for corals exposed to anomalously warm water. Ongoing research suggests that organic matter in turbid areas may absorb UV wavelengths and screen sunlight. Corals at these sites may be less susceptible to bleaching. However, turbid conditions are often sub-optimal for coral reef development, and biological diversity may be low in these areas.

4. Resistant and tolerant coral communities. Knowledge about the composition of coral communities can also help predict sites that are more resilient to bleaching. Observations during past bleaching events from around the world indicate that

certain types of corals are generally more resistant to bleaching than others⁸⁰. If a site is dominated by resistant species, then any temperature-induced bleaching is likely to be less severe (Box 4.1 in Section 4.2 shows key coral groups in order of bleaching resilience). Similarly, certain corals appear to be able to survive in a bleached state for an extended period and are, therefore, less likely to die even if they bleach. While less work has been done on bleaching tolerance, it appears that corals with a massive morphology and thick tissue, such as those from the families Poritidae, Favidae and Mussidae, have greater tolerance to bleaching¹¹⁸.

Another observation is that different colonies of the same species can vary in their bleaching response, and one mechanism that has been identified for this variation is differences in the types of zooxanthallae hosted within the coral tissue⁷⁹. Case study 7 describes work being done on the Mesoamerican reef to assess the importance of stress-tolerant zooxanthallae in determining the severity of bleaching as part of a broader initiative to identify potentially resilient areas.

5. High recovery rates. The ability to recover, and the rate of recovery, after a mass bleaching event is another relevant characteristic of coral reef resilience. Sites that recovered well from previous disturbances, such as storms, are more likely to recover quickly from bleaching events. Where recovery rates are not known, managers can infer a site's capacity for recovery by evaluating whether conditions are conducive to coral recruitment and survival.

Table 3.1 Characteristics and information sources for predicting the relative bleaching resilience of candidate reef sites

Availability of information sources will depend on level of resources or expertise, and are divided into low, moderate and high resource requirements.

I.Cooler due to upwelling or proximity to deep water

- Consult nautical almanacs, charts, local fishers, online NOAA resources', and University of Hawaii² website to identify and
 assess exposure to regional and local currents. Look at the location of islands and reefs to infer how prevailing currents
 might cause mixing and water-cooling.
- Local studies that release dye, use drogues, or release drift cards or floating instruments can give some information on surface current movements.
- Conduct shipboard studies of underwater and surface currents. Use oceanographic models of water movements.

2. Protected by shading

- Check topographic maps of islands and mainland coasts indicating likely areas of shading. In particular, look for high, steep
 islands and coasts with cliffs. Mapping of the ocean floor and the topography of the reef can be used to describe the aspect
 (angle to the sun) of particular reef faces.
- Direct observation of shading-by snorkellers and divers, from boats, or by time-lapse photography or video-can be used to quantify sun exposure. Correlation with the presence or absence of bleaching in shaded locations during or after a bleaching event can also indicate the impact of shading.
- Use a network of light meters to measure and correlate sunlight exposure over time with bleaching and mortality patterns.

3. Protected by screening by suspended particles and dissolved matter

- Use satellite imagery, aerial photos, or direct surveys to identify areas with consistently lower water clarity.
- Measure suspended sediments and turbidity along transects with a Secchi disc, turbidometer, or other instruments.
- Take scientific measurements of sunlight penetration and quantitative measurements of CDOMs.

4a. Coral community dominated by bleaching-'resistant' corals

- Compile existing data or local knowledge about composition of coral communities at candidate sites. Identify dominant coral groups and give them a bleaching resistance ranking based on Box 4.1.
- Conduct surveys of coral community composition at candidate sites and assess relative dominance of coral types known to be more resistant to bleaching.
- Conduct physiological studies of dominant corals at candidate sites to measure likely resistance indicators, such as zooxanthellae type and photoprotective pigments.

4b. Coral community dominated by bleaching-'tolerant' corals

- Compile existing data or local knowledge about composition of coral communities at candidate sites. Give dominant coral groups an indicative bleaching tolerance ranking based on morphology (massive > encrusting > branching/tabular) and tissue thickness or 'fleshiness'. Corals with good capacity for heterotrophic feeding should be assessed as having higher bleaching tolerance, where this information is known.
- Conduct surveys of coral community composition at candidate sites and assess relative dominance of coral types known to be more tolerant of bleaching (using criteria above).
- Conduct physiological studies of dominant corals at candidate sites to measure likely tolerance indicators, such as tissue condition (lipid levels) and heterotrophic capacity.

5. Demonstrated strong recovery

- Use existing data or local knowledge to identify areas with a good mix of old and young corals. Previous studies or anecdotal observations may help identify reefs that have rapidly recovered from other disturbances such as storm damage or COTS (Acanthaster) outbreaks.
- Undertake field surveys to identify those places where coral cover and species diversity quickly recovered following an
 earlier known bleaching event. Use point, line or quadrat survey methods to measure changes in coral cover and community
 composition following bleaching- induced mortality at candidate sites. The presence of high numbers and diversity of early
 coral recruits, and the prevalence of conditions known to be conducive to survival and growth of young corals, can also
 indicate strong recovery potential.
- Develop models to predict recovery capacity from ecological dynamics that include recovery-supporting processes, such as larval supply, connectivity and physico-chemical conditions that enhance coral survival and growth.

www.noaa.gov/

² www.soest.hawaii.edu

A major research program to improve predictions of coral bleaching in Palau

A collaborative program involving experts from The Nature Conservancy, the US National Oceanic and Atmospheric Administration (NOAA) and the Australian Institute of Marine Science is taking a detailed look at the role of sea surface temperature (SST) in major bleaching events. The goal of the project is to improve predictions of coral bleaching in Palau, but the knowledge gained from the study will be valuable to other regions.

Modelling patterns of thermal stress

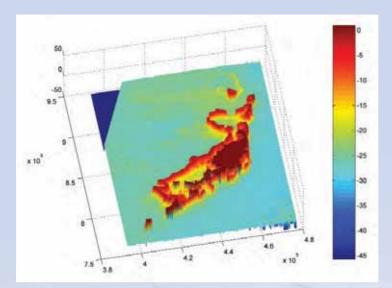
One of the major environmental stresses that cause bleaching of corals is heightened water temperature. Over 98 per cent of solar radiation energy is absorbed within the top four metres of the water column. This heat will stay at the top of the water column unless there is a mechanism to mix it with the cooler water below. Vertical mixing occurs in regions of relatively strong horizontal currents; these can be associated with surface winds, large-scale currents (for example the Gulf Stream) and tides. Therefore, extended periods of cloudless summer days with low winds and low currents create conditions known to induce bleaching events.

Hydrodynamic models can be used to predict SST patterns for a future, severe, mass coral bleaching event. Thus, they provide an excellent tool for managers, particularly when designing Marine Protected Area networks. Hydrodynamic modelling can also assist in the investigation of other issues that relate to the coral reef ecosystem. Connectivity with biological events (for example coral/fish spawning) and human activity (such as sewage outfall and pollution accidents) can be monitored and/or predicted.

Calibration and validation of the hydrodynamic models for the Palau project will be carried out by comparison of the model results with in situ data. Seventy instruments were deployed across the Palau lagoon to record data for a five-month period, from August 2003 to January 2004. The instruments included current meters, conductivity sensors, temperature profiles and pressure gauges. Atmospheric conditions were recorded during the same period using a dedicated weather station. In addition, vertical profiles of conductivity and temperature with depth were measured three times at several locations during the study.

One of the most important inputs to a high-resolution hydrodynamic model is the bathymetry. Since there was no reliable source of high-resolution bathymetry for Palau, this project endeavoured to generate one. This was achieved by merging a global bathymetry data set with satellite-derived depth data, and validating these with a series of transects collected from small boats.

CASE STUDY 6



Bathymetry map developed for Palau by merging global bathymetry data with satellite-derived depth information

Studies of bleaching events on the Great Barrier Reef, Australia, have demonstrated how the hydrodynamics during a coral bleaching event can be predicted with reasonable accuracy. The methods used in this study will be used to increase our understanding of the climatic and physical conditions conducive to rapid seawater warming to help understand the process of heat dissipation within lagoonal and barrier reef systems. It is expected that the study will highlight the importance of micro-environments, local topography, and reef hydrodynamics in determining the severity of bleaching during periods of anomalously high sea temperatures. In addition, during the Palau study, additional research is being undertaken to further develop the technology and capacity to predict coral bleaching events.

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Understanding patterns of bleaching in the mesoamerican reef – a collaborative effort to support resilience-based management

Bleaching on the Mesoamerican Reef

The Mesoamerican reef includes the longest barrier reef in the western hemisphere, with a diverse array of associated reef types. The core of this reef system, in Belize, did not suffer a major bleaching event until 1995, when approximately 10 per cent of colonies suffered at least partial mortality¹⁵⁵. More recently, there have been dramatic declines in live coral cover attributed to the 1997-98 bleaching, including severe mortality on nearly 100 per cent of central lagoonal reefs and 50 per cent of 12 fore-reef sites studied. These losses have been associated with the combined effects of bleaching and a hurricane^{156, 157}. Several regional threat assessments have identified the increased frequency of coral bleaching events associated with climate change as a primary threat to the region^{158, 159}.

A collaborative program

In response to concerns about the future of this reef ecosystem, the WWF, The Nature Conservancy (TNC), the Wildlife Conservation Society (WCS) and Scripps Institution of Oceanography are collaborating in an attempt to understand the variability in responses observed during past bleaching events. These agencies hope to determine whether this may provide a basis for resilience-based management of the region. This work will use TNC's Reef Resilience (R²) Toolkit to help design and field-test a conceptual model of reef resilience. The model will be based on natural variations in key environmental conditions and incorporate the latest research on reef connectivity.

Understanding the characteristics that actually confer resilience on any given reef will provide managers with specific targets for conservation. It will also provide one of the key criteria in ongoing efforts to develop and implement a full representational analysis of the region's Marine Protected Areas network. A variety of approaches will ultimately be needed to address this issue, but one novel avenue currently being studied by Scripps and the WWF involves the characterisation of the abundance and distribution of zooxanthellae in various reef habitats. Furthermore, knowledge about zooxanthellae distributions will assist managers to decide whether this approach could play a role in the design of management strategies.



Melanie McFie

Coral bleaching can be highly variable, even within a single coral colony

Variability in coral bleaching

Different coral species can vary substantially in their response to thermal stress, independent of zooxanthellae type⁸⁰. Yet, different colonies of the one species can also vary in their bleaching response, and one mechanism that has been identified for this variation is differences in the clades of zooxanthellae hosted within the coral tissue. Different clades of zooxanthellae respond differently to stress, leading to patterns of coral bleaching that often cannot be explained by coral taxonomy alone¹⁶⁰. Experimental bleaching of corals and studies of the distribution of zooxanthellae suggest two potential explanations for the observed patterns of bleaching^{161, 162}. The first is that corals may resist bleaching by associating with stress tolerant zooxanthellae. The second suggests that corals may be able to survive future bleaching events by repopulating with stress-tolerant zooxanthellae^{162, 163}.

Monitoring to understand resistance to bleaching

Beginning in 2003, researchers from the Scripps Institution of Oceanography and from the WWF, Belize, began surveying the presence of stress-tolerant zooxanthellae within reefs and in adjacent reef habitats. One theory that emerged from this survey is that the amount of bleaching that occurs at each reef may be influenced to some extent by the prevalence of stress-tolerant genotypes of zooxanthellae. Identifying the patterns and sources of zooxanthellae diversity will provide information on the role of zooxanthellae composition in determining the effects of thermal stress on coral communities, which may assist managers to evaluate the potential resilience of different sites.

Using research to help managers support reef resilience

Following bleaching events, researchers and managers will work together to assess the importance of stress-tolerant zooxanthellae in determining the severity of bleaching during future thermal stress events. Combining the monitoring of zooxanthellae diversity with other key factors for reef resilience will allow managers to better understand what makes a specific reef resilient. In turn, this will help them adapt management strategies so that the focus is on protecting those factors most important for maintaining reef resilience.

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3.3 Using Marine Protected Areas to increase resilience

Marine Protected Areas (MPAs) can help build coral reef resilience by supporting and enhancing the factors that confer resilience: good coral reef condition, biological diversity, connectivity, and favourable local conditions. Traditionally, principles of MPA selection, design and management have not specifically addressed

Expected increases in the extent and severity of mass coral bleaching warrants the inclusion of additional, resilience-related criteria in MPA site selection

the threat of mass coral bleaching⁸⁹. This section considers the additional considerations that are relevant to MPA site selection (Section 3.3.1) and management (Section 3.3.2) in the context of mass coral bleaching.

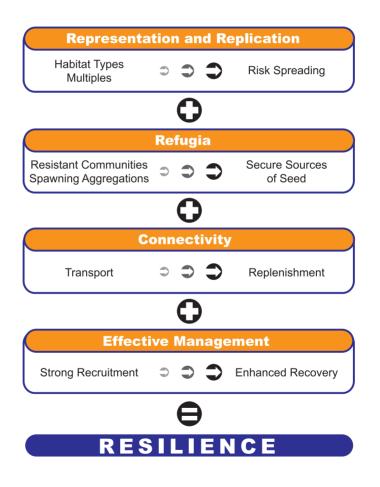


Figure 3.3 Principles for building resilience into MPA design

The Reef Resilience (R^2) Toolkit, developed by TNC, identifies four key principles to help incorporate coral reef resilience into MPA design (www.reefresilience.org).

3.3.1 Selecting MPA sites in the context of mass coral bleaching

Expected increases in the extent and severity of mass coral bleaching warrants the inclusion of additional, resilience-related criteria in MPA site selection (Figure 3.3). Importantly, the resilience principles outlined here are meant to build on existing MPA selection criteria and design principles, not to replace them. Existing MPA planning approaches, including appropriate stakeholder engagement strategies, remain essential for defining conservation objectives, identifying threats and determining management strategies to address these threats. The intention of these additional resilience principles is to enhance the role of selected sites in contributing to improved resilience of the ecosystem.

1. Representation and replication. Sometimes called 'spreading the risk', this principle recommends that, in the uncertain context of climate change, MPA network design should aim to replicate a range of reef types and related habitats. Section 3.1.2 describes how protecting biological diversity confers resilience to coral reefs. This principle aims to maximise biodiversity as a way of increasing the chance that among these species and habitats there will be enough survival and recovery to maintain functional coral reef ecosystems.

2. Refugia. The refugia principle aims to take advantage of coral reef areas of natural resilience, as identified in Section 3.2. In the context of mass coral bleaching, refugia can serve as 'seed banks' or source reefs for less resilient areas. For refugia to serve this role, they must be effectively protected from local stressors, such as anchor-damage, over-fishing or pollution, and thus are high priority for increased management attention.

3. Connectivity. Connectivity plays an important role in coral reef resilience by promoting recovery after mass coral bleaching events and other disturbances (see Section 3.1.2). Implementing this principle in MPA design involves considering prevailing currents and adjacent non-reef areas. Linking MPAs along prevailing, larvae-carrying currents can replenish downstream reefs, increasing the probability of recovery at multiple coral reef sites. Adjacent non-reef areas are important to connectivity because they can become important staging areas for coral recruits as they move between reefs and into new areas.

4. Effective management. Coral reef ecosystems in good condition are better able to survive and recover from mass bleaching events (see Section 3.1.2). This principle refers to effectively managing local stressors at a site in order to optimise coral reef condition. High coral cover, abundant fish populations and good water quality are all elements of coral reef ecosystem health that support recovery. To implement this principle, MPA selection should give priority to sites where levels of resource use and effective management can help maintain these supportive attributes.

3.3.2 Managing MPAs in the context of mass coral bleaching

Once sites are selected for inclusion in an MPA network, managers must decide on the management objectives and management regime for each protected area. Again, in the context of mass bleaching, management can increase reef resilience by strengthening or taking advantage of factors that confer resilience: good coral reef condition, biological diversity, connectivity and favourable local conditions^{90, 91}. Marine Protected Areas are

particularly suited to managing direct threats to coral reefs, such as those from over-fishing and recreational overuse or misuse. While MPAs can assist in addressing indirect threats, such as land-based pollution, achieving this goal usually requires broader management activities (see Section 3.4).

A high-level objective of MPA management in the context of resilience should be to protect fish abundance, with an emphasis on herbivorous fishes. The role of herbivores in maintaining conditions that are conducive to coral recruitment and survival³ makes their protection critical for reefs subject to increasing sea temperatures (see Section 2.5.2). While some level of harvest may be sustainable, the importance of herbivores to future reef resilience means that managers should carefully manage fishing activity to ensure adequate levels of herbivory are sustained (a conservation objective), and not merely to ensure a sustainable or maximum harvest (a fisheries objective)¹¹.

Managing the impacts of recreational use of MPAs is another way managers can support the resilience of reef ecosystems. Recreational activities can result in physical damage from diving and boat anchoring, and from release of nutrients and combustion products from vessels (see Section 2.5.2). Where MPAs have been established to protect important bleaching refugia, even localised stresses associated with recreational activities may pose a significant threat to resilience. MPA managers should carefully control snorkelling, diving and boat usage to minimise stress to corals, especially during or following a bleaching event. In most cases, these are sites within MPAs and/or sites with high visitation rates. While MPA managers may already have regulations and best-practice guidelines in place, measures to ensure users avoid imposing additional stresses during periods of temperature stress should be considered.

3.4 Broader management interventions to increase resilience

Many managers have a range of authorities and tools that can be used to protect resilient reef areas from local stressors and to increase coral reef resilience. These include fishery regulations, tourism permitting, coastal development regulations and watershed management. Expected increases in the frequency, spatial extent and severity of mass coral bleaching events will have implications for effective application of these traditional management tools. At present, these implications are largely understood as conceptual principles that will benefit from refinement with additional experience and research. The approach taken by The Republic of the Seychelles following the 1997-98 mass bleaching event, described in case study 8, is a good example of how these principles can be put into practice.

Identifying resilient areas for improved protection of Coral Reefs of the Seychelles

Responding to the devastating impacts of coral bleaching in the Seychelles

The Republic of the Seychelles, located in the western Indian Ocean between 4° and 11° south of the Equator, was one of the areas most severely affected by the global mass bleaching episode of 1997-98. In this area, sea temperatures exceeded 30°C for several months. Coral mortality due to bleaching was extremely high, with declines of 85-95 per cent in the cover of structurally dominant branching corals (*Acropora* and *Pocillopora*) on the reefs surrounding the inner granitic islands of the group. These islands, Mahé, Praslin and La Digue, are home to 95 per cent of the population of the Seychelles.



Sailing and other reef-oriented tourism activities are an important use of coral reefs in the Seychelles

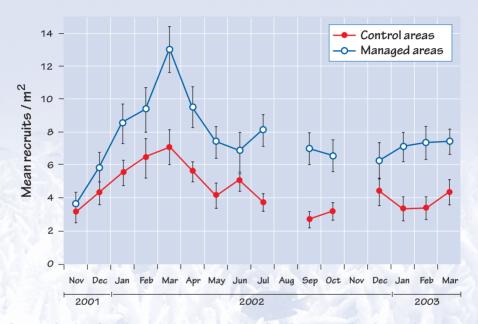
In the Seychelles, coral reefs are particularly important to social and economic sustainability. Following the 1998 event, the Government immediately initiated a collaborative program to facilitate and promote the recovery of damaged reefs, and to identify focal sites for future conservation efforts. The program focused on rebuilding the resilience of reefs in the region. The Seychelles Marine Ecosystem Management Project (SEYMEMP) was established to facilitate the recovery of coral reefs, guide the management of existing marine protected areas (MPAs) and develop strategies to improve the protection of reefs against future coral bleaching events, or other negative impacts. Major aims for SEYMEMP included:

- assessment of the impacts of the 1997-98 coral bleaching event on corals and associated fish communities
- identification of areas resistant to bleaching, and of areas that have demonstrated strong recovery
- investigation of factors that could interfere with coral reef recovery and the development of tools and strategies to promote recovery of degraded reefs.

Some sites are showing signs of resilience

Detailed ecological monitoring of benthic transects since the 1997-98 coral bleaching event have identified reef sites that are demonstrating good recovery. These sites are showing strong trends in the increase of hard coral cover, increasing from an average of less than five per cent to 15-20 per cent in six years. This compares to an average of 10 per cent cover

after six years for all sites combined. Hard coral diversity has also shown strong signs of recovery at these sites, with many now having a significant proportion of the species typical for the region. Significantly, however, the reefs of the Seychelles were affected by bleaching events again in 2003 and 2004, impeding or reversing recovery at many sites. There was an interesting contrast in the effect of these more recent events on *Acropora* and *Pocillopora* corals, with the latter showing a strong decline in recovery rates while the recovery trajectory for *Acropora* (pooled across species) was generally unaffected.



Average density of coral recruits in managed areas (urchins removed) and control areas (urchins not removed)

This graph shows the mean number of acroporid and pocilloporid coral recruits per 1 m^2 (0-5 cm size class) in areas subject to high grazing pressure by black-spined sea urchins (control areas, red line), and areas where sea urchin densities were maintained at a lower level through active population management (managed areas, blue line).

Coral recovery is threatened by overgrazing

At many sites, the distribution and density of grazing sea urchins (*Diadema* spp. and *Echinometra* spp.) appears to have increased in recent years. This is believed to be due to the reduction in the number of fishes known to prey on these mobile invertebrates. Grazing of hard substrate by urchins affects recruitment of hard corals because settling larvae are consumed along with the targeted algae. At locations where grazing is intense, recovery is limited, or inhibited entirely. Experimental efforts to control sea urchin density proved to be effective in increasing coral recruitment, with a doubling in the abundance of *Acropora* and *Pocillopora* recruits over a 12-month period in areas where urchins were removed, as compared to control areas. Consequently, reef managers are considering control of sea urchin populations to facilitate recovery within MPAs. Priority areas for this management response are close to coral communities with a demonstrated resilience to bleaching, either by surviving the bleaching event with minimal mortality, or by rapidly recovering.

Some sites were protected by proximity to upwelling

Three reef sites with the fastest rates of recovery–Marianne Island Reef, Aride Island Reef and Anse Petit Cour Reef at Praslin–suffered minimal coral mortality. This resistance occurred despite the sites being characterised by a relatively diverse community of hard coral species, many of which did not survive elsewhere. It is probable that these sites benefited from cold-water upwelling, and they are likely to be important seed sources for replenishment of depleted coral communities. These refugia are being considered for special management measures designed to improve the resilience of the entire system following impacts from future bleaching events.

Management actions to protect coral refugia

Some of the sites shown to have higher resilience to repeated bleaching events are outside the boundaries of existing MPAs, indicating that there is value in considering increased protection of these sites through future incorporation into the MPA network in the Seychelles.

One site identified as a refuge from bleaching-induced mortality is already protected within an MPA, but was being threatened by anchor damage associated with heavy tourism use. Moorings have been installed to minimise anchoring in the area, and ongoing monitoring has shown that, as a result, the damage to coral has been significantly reduced.

This case study demonstrates the importance of regular monitoring and adaptive management in responding to emerging threats, such as coral bleaching. The strong partnerships among government agencies, non-government organisations and stakeholders and local communities have resulted in a better understanding of the effects of past coral bleaching events, and identified strategies to support reef resilience. This initiative provides the foundation for efforts that will help the reefs of the Seychelles to continue recovering from the mass bleaching events.

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3.4.1 Guiding principles

The following three principles were identified by participants of an international workshop on 'Coral Reefs, Climate Change, and Coral Bleaching' that was hosted by the US government in 2003. At the workshop, a group of experts was brought together to suggest how mass coral bleaching could be integrated into broader coral reef management efforts given the existing limitations in our scientific understanding. Their recommendation was to manage adaptively for the factors that confer resilience and the cumulative effects of multiple stressors.

Manage for the factors that confer resilience. Broader reef management efforts have a key role to play in supporting the factors that confer reef resilience (see Section3.1.2). In particular, efforts to address indirect threats to reefs that degrade coral reef condition can normally not be achieved through MPAs alone and require integrated, collaborative coastal management. Examples of indirect threats include degraded water quality that might result from coastal development or agricultural land use.

Recognise the cumulative effects of multiple stressors. Under the additional threat of mass coral bleaching, management of localised stressors may need to become more conservative in order to help maintain ecological condition and services. Managers need to consider how targets for and expectations of fish abundance, water quality, and physical damage from recreational use might be revised to reflect the cumulative impacts of global and local stressors. Ecological modelling can assist managers in this process by identifying the relative importance of different management goals (Box 3.1).

Manage adaptively. A key issue for implementation of broader measures to build reef resilience is the limited information available. Current understanding of the factors that confer resilience is based largely on scientific principles, rather than empirical studies. The importance of maintaining high coral cover, abundant herbivore populations and good water quality in promoting resilience is widely acknowledged (see Section 4.2.3).Yet, the complexity of the ecosystem and the state of scientific knowledge mean that managers must continue to make pragmatic decisions and implement management actions in an environment of considerable uncertainty.

The adaptive management approach provides a valuable framework for active management in the face of uncertainty^{40,78}. It may be particularly appropriate in the context of coral bleaching where there is a strong imperative to respond to a highly visual event despite the absence of complete knowledge. Adaptive management recognises that management actions can be taken in a hypothesis-driven framework where management is an

Taking an adaptive management approach to managing reefs in the context of climate change can help foster innovation and collaboration in management that accelerates progress in identifying productive future strategies

iterative learning exercise rather than a 'solution' to a well understood problem. Reflecting on what has been learned at each stage of the management process provides insights about how future management actions can be refined or 'adapted'. Adaptive management can also be helpful in fostering innovation and collaboration in management, attributes that are likely to accelerate progress in identifying productive approaches to future management in the context of mass coral bleaching.

Box 3.1 Using models in coral reef management

The processes driving coral reefs occur on a wide range of spatial and temporal scales. Given the complexity of such systems, there is an increasing need to use models to answer some of the questions posed by managers. For example, an empirical study is unlikely to deliver a prompt answer to the question, 'What level of fishing pressure can be tolerated given scenarios of increasing sea temperature and cyclone activity?'. However, in constructing answers, models can be a powerful asset when used in combination with good empirical data.

Models have two main uses in science. First, they help us understand the relative importance of single factors in the dynamics of complex systems (sensitivity analysis). The modeller may create a simplified version of the reef and then test the plausibility of alternative scientific explanations, or the relative effectiveness of different management scenarios. For example, managers may use a model to investigate how changing one condition (for example the abundance of herbivores) can influence the rate of recovery on a reef impacted by coral bleaching. Moreover, a variety of factors can be modified in tandem to investigate whether certain combinations affect the reef's recovery more than others do. These models can identify critical aspects of the ecosystem that disproportionately influence reef resilience. Managers can then consider how to reduce stress at these critical parts of the system.

The second use of models is that of prediction. For example, given our present ecological understanding of scenarios for future climates, what percentage coral cover will be found on local reefs in 2050? Although models based on ecological data can be used for prediction, there are many scale issues to consider. For example, it is difficult to reconcile the impact of a warming climate with the daily foraging of parrotfishes within a single model. Therefore, different types of models are appropriate for different questions, and an optimal solution would use a range of inter-connected models at different scales. In general, predictive models need a firm basis in probability so that the confidence in the predictions is made abundantly clear.

Modelling the conditions on reefs in relation to coral bleaching and management strategies is a very active, but relatively new, area of research. Whilst a number of groups are working on various models, few results have yet been published. The paper by Woodridge et al (2005)⁴⁷ illustrates the potential of modelling to support resilience-based management in the context of coral bleaching. Further information can be found from individual research groups including AIMS Reef Futures (www.aims.gov.au/reeffutures), the Marine Spatial Ecology Lab (www.ex.ac.uk/msel) and the National Centre for Caribbean Coral Reef Research (NCORE, www.ncoremiami.org).

3.5 Reef restoration strategies

Recent worldwide reports of reef damage due to mass bleaching events, combined with projections of future warming trends, indicate that reef managers should expect reefs to continue to deteriorate^{5.9}. Although the natural resilience of reef ecosystems will facilitate recolonisation and subsequent recovery of sites that suffer significant coral mortality, full recovery to pre-disturbance coral cover and diversity can be an extended process, requiring many years, and usually many decades^{133,134}. The recovery process can be further lengthened, and even inhibited, if the natural resilience of the reef ecosystem has been eroded through other pressures, such as excess nutrients or sediments, habitat damage or over-harvesting of key functional groups^{88,93}.

In some instances, following severe bleaching-related coral mortality, reef managers may wish to consider proposals to assist or accelerate natural recovery processes through active restoration. Many techniques come under the banner of reef restoration. Some of these techniques are only appropriate in very specific circumstances. Care must be taken to use only those techniques appropriate to the reef in question and to the nature of the disturbance that has affected it.

In some instances, following severe bleaching-related coral mortality, managers may wish to consider assisting natural recovery through active restoration

The logistics, costs and effectiveness of restoration activities as well as any legal considerations should be carefully examined before deciding on a course of action⁹⁴. Cost-effective approaches and technologies are still in the early stages of development, and, in most cases, are currently not viable for implementation on large spatial scales. Given the extreme cost of some of the techniques, especially coral transplantation, careful consideration is needed when deciding whether to use available funds for restoration of a small area or for initiatives with broader influence, such as education and preventative measures.

The diversity and scale of experimental restoration approaches used to date vary widely⁹⁴. They cover habitat modification, coral transplantation, species re-introduction and enhancement of recruitment. Some of these interventions involve large-scale, sub-tidal structures designed to facilitate natural colonisation of reef-related species⁹⁵⁻⁹⁷, while others use simpler and less costly approaches that are more readily replicated⁹⁸⁻¹⁰⁰. The following sections examine restoration issues in detail.

3.5.1 Considerations for reef restoration strategies

Several overarching considerations are central in deciding whether to pursue restoration strategies. These include: Is restoration the best use of limited resources? Will restoration efforts endure in the long-term, given the expected recurrence of bleaching? Will restoration efforts be effective under the current and expected regime of other stresses? Is there legal or socioeconomic justification for the undertaking of restoration? This section examines these issues in more detail with the aim of assisting managers to make decisions on the use of restoration measures in response to coral bleaching events.

Before implementing restoration, managers should evaluate whether selected strategies will be costeffective, endure in the long-term and are able to achieve desired results Is restoration the best use of resources? Restoration of coral reefs is an extremely expensive exercise¹⁰¹. For example, the costs for extensive restoration efforts following ship groundings have ranged from US\$10 000 to an estimated US\$6.5 million per hectare¹⁰². If there is no need to repair structural damage, and only coral

transplantations are carried out, the costs can be much lower. However, even in these situations, it is likely to cost tens of thousand of dollars per hectare just to achieve a realistic target of 10 per cent coral replacement cover¹⁰³. Furthermore, these costs are based on trials in which only a few fast-growing genera, with high aesthetic values and fast growth rates (such as *Acropora* and *Pocillopora*) were used¹⁰³⁻¹⁰⁵.

In light of the immense costs that are involved in coral transplantation, the ethics and appropriateness of spending resources for such small-scale projects must also be considered. The largest coral transplantation projects carried out to date involved an area of 7.1 hectares, which highlights the limited scale over which transplantation techniques can be applied. A relatively cost-effective approach using rock piles has been recently demonstrated in Komodo (Indonesia) over a six hectare area, suggesting potential for rehabilitation of larger areas¹⁰⁶. Yet, these spatial scales are still extremely small compared with the scale of damage that can result from mass bleaching events. Nevertheless, restoration strategies may continue to be appropriate for small sites of high value, such as significant tourist destinations. Even in these circumstances, however, managers will want to be sure that restoration efforts will result in lasting improvements.

Will restoration efforts endure? Even if funding and technical constraints were to be overcome, investment in coral reef restoration efforts will be wasted if chronic stresses that could be exacerbating coral mortality or hindering recovery are not managed. Mass coral bleaching is expected to be a recurrent phenomenon over coming decades, making it probable that restored sites will, in the near future, suffer a similar disturbance to that which motivated the restoration effort. Two approaches can be adopted, both based on current understandings of restoration and specifically addressing degradation caused by bleaching. For reefs that have survived past bleaching events, restoration can target the enhancement of resilience by promoting biodiversity. For reefs with a poor recovery record from bleaching, restoration should aim at promoting growth of tolerant species and providing shading against increased solar radiation.

Will restoration efforts be effective? Numerous experiments and case studies of reef restoration indicate the difficulty in achieving restoration success. Technical and financial constraints force a bias toward fast-growing coral genera in restoration projects, making it very unlikely that direct restoration will restore the impacted resource to a level that is functionally equivalent to pre-disturbance conditions. Furthermore, the survivability of transplanted corals is variable and subject to many factors beyond human control, leading to uncertain ecological outcomes.

3.5.2 Restoration methods

Direct, site-based restoration efforts that might be contemplated in response to bleachinginduced mortality can be divided into three main categories: coral transplantation, 'seeding' with coral larvae and reinstatement of herbivores. The potential benefits and limitations of each of these are discussed below.

Coral transplantation. An examination of case studies demonstrates that most aspects of coral reef restoration, coral transplantation in particular, are still at an experimental stage. The limited-scale projects implemented to date demonstrate clearly that coral transplantation is a very costly exercise, with uncertain ecological outcomes^{103,104}. In fact, coral transplantation introduces the risk of adverse outcomes, such as shifts in community structure, the transfer or introduction of diseases, or interference with the natural gene flow, and impacts on the donor colony or reef¹⁰⁵. Harm to existing corals and reefs can be minimised by using in situ coral mariculture to supply transplantation operations with corals adapted to natural reef conditions. The viability of in situ nurseries¹⁰⁷ has been demonstrated with propagation of loosely-scattered colonies in a sheltered, lagoon-like reef area¹⁰⁸. Yet, even at small spatial scales, the costs and benefits of coral transplantation require careful consideration before it is used for reef management purposes. Over spatial scales normally affected by mass coral bleaching events, coral transplantation is extremely unlikely to be financially viable.

In summary, coral transplantation should be viewed as a strategy of last resort, and should only be undertaken at small, high value sites where there is strong justification for accelerating natural recovery processes. If natural recovery is hindered by other stresses, such as poor water quality or excessive algal growth, management efforts should be prioritised to address these issues before investment is made in coral transplantation.

Coral 'seeding'. An alternative method to transplanting adult colonies to accelerate recovery is 'coral seeding'. This technique involves collecting larval slicks from broadcast spawners for direct transfer to an impoverished site, or 'staging' the slicks in protected habitats to allow larvae to settle before transferring to the target site¹⁰⁹. Coral larvae may also be reared under laboratory conditions until they are competent to settle, and then released into eddies associated with target reefs. Larval retention times of 1-3 weeks inside eddies are believed to promote enhanced local settlement. Although untested, proponents of this technique have suggested that coral seeding will result in regeneration rates of possibly two orders of magnitude higher than can be achieved by transplantation efforts¹⁰⁹.

Several concerns are relevant to coral seeding as a restoration technique. The method has not been widely tested, so its effectiveness in different circumstances is not well known. The practicalities of the method, especially in relation to costs, logistical requirements and expertise have not been explored for a range of settings. The ability of seeding to assist recovery to full (pre-disturbance) species diversity is not known, but is likely to be significantly limited. Furthermore, in most situations, damaged reefs will be supplied with natural sources of coral larvae from upstream source reefs, particularly when management schemes promote habitat connectivity. Coral seeding is only likely to be warranted in situations where a reef is very remote or has only limited connections with upstream sources of larvae. In summary, coral seeding techniques are still largely in the developmental stage, and present many of the concerns and limitations associated with coral transplantation. However, with further development and in some limited circumstances, they may prove to be a more cost-effective method for increasing recovery at defined sites¹⁰⁹.

Reinstate herbivores. In some situations, natural recovery of reefs following bleachinginduced mortality may be hindered by excessive growth of filamentous or fleshy algae⁴⁵. On many reefs, over-harvesting of herbivores, especially fishes, can lead to excessive algal growth⁴². This, in turn, results in reduced availability of the bare substrate required for settlement of coral larvae.

While the effects of reduced herbivory may not be obvious in an intact coral community, the effects of low recruitment rates resulting from excessive algal growth may be severe following a major disturbance such as bleaching-induced mortality⁴⁴. Although the overharvesting of herbivores from a coral reef system should be of concern to reef managers for a diversity of reasons, the effects of a coral bleaching event can dramatically increase the urgency of efforts to address this problem¹¹.

Widespread mortality of corals should trigger renewed efforts to prevent further, unsustainable, removal of herbivores from the system. This could entail greater limits on fishing activities or increased penalties for non-compliance with fishing restrictions. However, in situations where herbivore populations are already depressed due to heavy harvesting, passive management (such as the removal of fishing pressure) may not be enough to ensure herbivore populations recover. This is particularly relevant in locations where reef recovery is limited by excessive algal growth caused by chronically depressed herbivore populations. This might require captive rearing of herbivores, or perhaps methods of enhancing reproduction and recruitment of key herbivore species. Importantly, techniques of actively restoring herbivore populations remain to be tested, and the feasibility of this method requires further investigation.