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Resistance And Resilience To Coral Bleaching: Implications For Coral Reef Conservation And Management

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Abstract

The massive scale of the 1997-1998 El Niño-associated coral bleaching event underscores the need for strategies to mitigate biodiversity losses resulting from temperature-induced coral mortality. As baseline sea surface temperatures continue to rise, climate change may represent the single greatest threat to coral reefs worldwide. In response, one strategy might be to identify: (1) specific reef areas where natural environmental conditions are likely to result in low or negligible temperature-related bleaching and mortality (i.e., areas of natural “resistance” to bleaching) and (2) reef areas where environmental conditions are likely to result in maximum recovery of reef communities after bleaching mortality has occurred (i.e., areas of natural community “resilience”). These “target areas”, where environmental conditions appear to boost resistance and resilience during and after large-scale bleaching events, could then be incorporated into strategic networks of marine protected areas designed to maximize conservation of global coral reef biodiversity. Based on evidence from the literature and systematically compiled observations from researchers in the field, this paper identifies likely environmental correlates of resistance and resilience to coral bleaching, including factors that: reduce temperature stress, enhance water movement, decrease light stress, correlate with physiological tolerance, and provide physical or biological enhancement of recovery potential. As a tool for identifying reef areas that are likely to be most robust in the face of continuing climate change and for determining priority areas for reducing direct anthropogenic impacts, this information has important implications for coral reef conservation and management.

Introduction

It is now generally acknowledged that coral reefs are among the most threatened global ecosystems, as well as among the most vital (Costanza et al. 1997; Bryant et al. 1998; Boesch et al. 2000; Reaser et al. 2000; Wilkinson 2000). Reefs are of critical importance to human survival (especially in developing countries) as they provide subsistence food for a substantial portion of the population, serve as the principle coastal protection structures for most tropical islands, and contribute major income and foreign exchange earnings from tourism (Costanza et al. 1997; Wells et al. 2001; Salm et al. 2001). The value of living resources (such as fisheries) and services (such as tourism returns and coastal protection) provided by reefs has been estimated at about $375 billion annually (Costanza et al. 1997). In addition, coral reefs provide habitat for some of the greatest biological diversity in the world (Ray 1988).

Reef-building (Scleractinian) corals are highly dependent on their symbiotic single-celled algae (zooxanthellae), which provide up to 95% of the corals' carbon requirements for growth, reproduction, and maintenance (Muscatine 1990). Corals and their zooxanthellae are vulnerable to a variety of environmental stressors that can disrupt the symbiotic relationship and cause "bleaching", or loss of zooxanthellae and their photosynthetic pigments. Bleaching stressors can include freshwater flooding (Goreau 1964; Egana & DiSalvo 1982), pollution (Jones 1997; Jones & Steven 1997), sedimentation (Meehan & Ostrander 1997), disease (Kushmaro et al. 1997; Benin et al. 2000), increased or decreased light (Lesser et al. 1990; Gleason & Wellington 1993), and especially elevated or decreased sea surface temperatures (Glynn 1993; Brown 1997; Hoegh-Guldberg 1999). During a severe bleaching event, corals may lose 60-90% of their zooxanthellae, and the remaining zooxanthellae may lose 50-80% of their photosynthetic pigments (Glynn 1996).

Once the stress subsides, corals can often recover and regain their previous levels of zooxanthellae; however, this depends on the intensity and duration of the stress (Hoegh-Guldberg 1999). Prolonged or extreme exposure can result in mortality of not only individual corals but also whole assemblages or reef tracts (Wilkinson 1998, 2000). Furthermore, coral colonies that have been stressed and suffered partial or complete mortality may be more vulnerable to algal overgrowth (Done 1992) and diseases (Kushmaro et al. 1997; Harvell et al. 2001, 2002), which can lead to further losses.

Reef areas that have suffered mass mortalities eventually begin to disintegrate as physical and biological erosion outpace calcium carbonate accretion by remaining corals (Done 1992). Loss of structural complexity from reef disintegration, combined with overgrowth by algae and lack of recruitment success on damaged reefs, can lead to dramatically altered patterns of coral species composition, and even complete restructuring of communities; such shifts have occurred after events (sometimes working in combination with each other) such as cyclones, outbreaks of predatory Crown-of-thorns starfish, disease epizootics, and bleaching events (Done 1992; Hughes 1994; Shulman & Robertson 1996; Ostrander et al. 2000). In some cases, coral bleaching has resulted in local species extirpations and species richness declines (Aronson et al. 2000; Glynn et al. 2001; Loya et al. 2001).

Depending on the type and extent of the stressor(s), coral bleaching can be localized, or widespread over large geographic scales. Salm et al. (2001) point out that localized bleaching events are often due to direct anthropogenic stressors (e.g., pollution or freshwater runoff), which can be prevented through abatement of the stress at its source. In these cases, poor management practices in adjacent riparian zones can be corrected (e.g., reforestation and other erosion and flood control measures) in order to minimize the threat at its origin.

Unlike the localized bleaching events described above, large-scale bleaching events can not be fully explained by localized stress factors and instead have been strongly linked to the presence of increased sea surface temperatures at regional scales (Glynn 1993; Wilkinson 1998, 2000). These large-scale events have increased in frequency and severity over the last two decades (Wellington et al. 2001), and in 1997-1998, the distribution of anomalously high sea surface temperatures (or *HotSpots*; Goreau & Hayes 1994) and subsequent bleaching coincided with the largest El Niño-Southern Oscillation (ENSO) on record. Bleaching spanned the tropics in over 50 countries, reflecting the global nature of the event (Wilkinson 1998, 2000), with observations by field scientists of 70-99% mortality at some sites in the Arabian Gulf, Maldives, and Seychelles (Goreau et al. 2000) and almost total mortality of the dominant space-occupier (*Agaricia tenuifolia*) in lagoonal shoal reefs in Belize (Aronson et al. 2000). If average temperatures continue to increase due to global climate change, then corals will likely suffer even more frequent and severe bleaching events in the future. Thus, climate change may now be the single greatest threat to reefs worldwide.

From a manager's perspective, increases in sea surface temperatures linked to climate change can not be readily addressed at the source to control the stress, at least not in a sufficiently rapid time frame given the severity of the bleaching threat. This is due to the lag time in ocean temperature response, which would result in continued ocean warming over the next century even if atmospheric CO_2 concentrations were to be stabilized today (Albritton et al. 2001). However, there may be actions that managers can take at local scales (at the scale of reef patches, assemblages or tracts) to enhance the capacity of reef systems to persist in the face of a changing climate. While mass bleaching conditions are generated by large-scale weather conditions, the bleaching response itself can be extremely patchy at local scales. Taking note of this, Salm et al. (2001) proposed that through thoughtful planning and strategic care of reefs within existing and future marine protected areas (MPAs)[1], it may be possible to take advantage of natural properties of coral reef ecosystems to mitigate the negative impact of bleaching on coral reef biodiversity in two broad ways:

(1) Identify and manage specific patches of reef where local conditions are likely to result in reduced temperature-related bleaching and mortality (i.e., coral assemblages with a high level of "resistance") to protect them from direct anthropogenic impacts and;

(2) Enhance the capacity for coral reef recovery ("resilience") by maintaining conditions that are optimal for larval dispersal and recruitment to damaged sites. This will require minimizing other stresses at these sites (abatement of direct localized impacts) and analyzing larval dispersal (connectivity) to maximize

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[1] We interpret MPAs in the broadest context as defined by IUCN-The World Conservation Union (Kelleher 1999): any area of intertidal or subtidal terrain, together with its overlying water and associated flora, fauna, historical and cultural features, which has been reserved by law or other effective means to protect part or all of the enclosed environment.

recolonization.

An understanding of which local environmental factors are predictors of greatest resistance and resilience to coral bleaching would help managers to identify, design and manage networks of MPAs in order to maximize overall survival of the world's coral reefs in the face of global climate change. The most useful approach would be one that utilizes natural processes rather than expensive technological fixes and helps managers to focus local management and enforcement efforts on the most critical areas. Given the limited capacity and funding available for management in many coral reef countries, what is especially needed are simple tractable strategies that any manager could begin to adopt immediately to maximize long-term survival of the broadest range of coral communities and reef types.

It is important to note that we are confining our discussion to local-scale resistance that occurs despite the presence of “mass bleaching conditions” in an area or region. This resistance is distinct from avoidance, where large areas or regions may never be tested by bleaching conditions at all due to larger-scale climatological and oceanographic phenomena (Done 2001). While the latter is an important area of ongoing research, the current paper focuses on determinants of local scale resistance within areas or regions that have experienced bleaching conditions, as this is an important scale at which local managers work. Therefore, building upon the work of Salm (2001) and West (2001), and further developing ideas discussed at a Workshop on Mitigating Coral Bleaching Impact Through MPA Design (Salm & Coles 2001), this paper identifies potential determinants of resistance and resilience to coral bleaching at the local scale and discusses their implications for coral reef conservation through MPA management. Patterns of coral bleaching and related mortality observed after the 1997-1998 ENSO provide some insights into where to begin.

Resistance and Resilience

During coral bleaching events, there is never total elimination of all corals on an entire reef; even in the severest cases, scattered colonies and patches of reef survive (i.e., show resistance). This became especially evident after the 1997-1998 bleaching event, as increasing numbers of researchers reported on a variety of sites in different regions where coral assemblages appeared to have resisted bleaching mortality compared to surrounding assemblages (Table 1). One goal, then, could be to systematically and comprehensively identify for further testing the potential determinants of these “pockets of resistance”, where local environmental conditions appear to boost coral survivability during large-scale bleaching events.

For the purposes of this paper, the term *resistance* refers to the ability of individual corals to resist bleaching, or to survive after they have been bleached. Such resistance may be due to either or both of the following: (1) intrinsic, species- or colony-specific physiological tolerance and (2) extrinsic environmental factors that afford some (but not necessarily full) protection from bleaching conditions, such that a subset of corals have a higher probability of surviving bleaching events. In the case of condition (1), *resistance* corresponds with Done’s (1999) use of physiological “tolerance” to describe persistence in the face of disturbance such that individual corals survive (although sub-lethal bleaching may occur). Condition (2) extends the definition of *resistance* to include situations where localized environmental factors serve to boost resistance of a coral assemblage, whether or not the individual corals have any intrinsic physiological tolerance. In this case, resistance refers to environmentally provided (extrinsic) counteraction of bleaching through partial moderation of bleaching conditions.

If mass coral bleaching and associated mortality of a subset of coral colonies in a community does occur, then coral reef systems can differ in their *resilience,* or ability to return to their previous state of diversity and abundance. We are using a narrower view of resilience than that expressed by Nyström & Folke (2001), who consider it in the context of ecosystems with multiple stable states responding to change through their ability to absorb disturbance, recover or reorganize, and adapt to different circumstances. Gunderson (2000) and Nyström et al. (2000) discuss resilience in terms of the speed of return to equilibrium after a disturbance and the magnitude of disturbance that can be absorbed by a system before it shifts from one stable state to another. Thus, we use resilience in reference to the ability of reef communities to regenerate to their previous state through growth and reproduction of surviving corals and through successful larval recruitment from within the area or from adjacent areas. The environmental conditions that favor such community resilience may be different from those that favor resistance.

Environmental Factors that Correlate with Bleaching Resistance

High sea surface temperatures and solar radiation are major stressors that interact to cause severe coral bleaching and mortality, and are responsible (either alone or in combination) for the majority of global-scale coral reef disturbances (Glynn 2000; Fitt et al. 2001; Wellington et al. 2001). Therefore, resistance to coral bleaching may be enhanced by any environmental factor that reduces temperature, blocks irradiance levels reaching corals, or both. Furthermore, since one of the results of bleaching is the production of toxic free radicals (Nakamura & van Woesik 2001), corals that are flushed by high volumes of water may also be at an advantage (see below). Finally, there may be environmental characteristics that favor pre-adaptation (physiological tolerance) of corals to resist coral bleaching – such as the presence of regularly stressful environmental conditions, e.g., periods of elevated solar radiation prior to sea-temperature warming events (Brown et al. 2000; Dunne & Brown 2001). Based on this information and on numerous observations by researchers after the 1997-1998 ENSO and other bleaching events, we can break down the determinants of resistance to bleaching into four broad categories: physical factors that reduce temperature stress; physical factors that enhance water movement and flush toxins; physical factors that decrease light stress; and factors that correlate with bleaching tolerance.

Physical Factors that Reduce Temperature Stress

Traditionally, areas of large-scale, cold-water upwelling spanning hundreds of kilometers have been cited as a main cause of poor development or absence of coral reefs, as in, for example, parts of the tropical eastern Pacific (Glynn & D'Croz 1990). However, the severity of coral mortality caused by high-temperature bleaching events appears to be far greater than that due to upwelling (Glynn & D'Croz 1990), and small-scale, localized upwelling areas spanning tens to hundreds of meters can cool heated surface water and protect reefs that would otherwise bleach during regional ENSO events.

In Vietnam, the rapid recovery of reefs from the 1998 bleaching at north Binh Thuan was attributed to the annual upwelling, which brought cold waters to the surface (Chou 2000). Reefs elsewhere in Vietnam recovered at a slower rate, implying that reefs near upwelling areas may suffer less from bleaching events. Goreau et al. (2000) cited observations by local scientists that many central Indonesian reefs and certain locations in the Maldives and Western Zanzibar were largely spared from severe bleaching in 1997-1998, apparently because of upwelling. In an area of local upwelling in the Sultanate of Oman, corals bleached immediately and comprehensively when sea surface temperatures reached 39 degrees Celsius, but within days, the temperature had fallen back down to 29 degrees, and the corals recovered completely over time (Salm 1993; Salm et al. 1993).

Unfortunately, oceanic processes and winds that sometimes generate upwelling can also produce alternative conditions that have the opposite effect, worsening the severity of bleaching. For instance, Jokiel & Coles (1990) describe meso-scale eddies that regularly develop in the lee of Maui and Hawaii during the summer months due to prevailing current and wind patterns. Such gyres can persist for months, stratify, heat 1 to 2 ^{o}C above the temperature of surrounding waters, and cause coral bleaching. Furthermore, usual patterns of upwelling can sometimes be *disrupted* during ENSO events, when high-pressure systems suppress currents and generate doldrum conditions. Therefore, targeting of upwelling areas as potential sites of survival should be balanced with consideration of whether the upwelling might be disrupted during ENSO events.

This is especially true in light of evidence that corals in upwelling areas may be more sensitive to temperature increases than their counterparts in non-upwelling areas. Glynn & D'Croz (1990) found that experimental high temperatures had a greater negative effect on corals from the Gulf of Panama, which experiences seasonally cool upwelling, compared to corals in the non-upwelling Gulf of Chiriqui. During the 1982-1983 ENSO event, warming in the Gulf of Panama was delayed by 3 months compared to the Gulf of Chiriqui due to local seasonal upwelling. However, while this seasonal upwelling protected Gulf of Panama corals initially, these corals were highly vulnerable to the persistent ENSO that extended beyond the protective upwelling period. Thus, the timing and persistence of upwelling with respect to ENSOs or other sea surface temperature anomalies should be considered when targeting areas most likely to survive mass bleaching events.

Physical Factors that Enhance Water Movement and Flush Toxins

Meso-scale oceanographic processes can sometimes counteract coral bleaching conditions at local scales: for example, the “island mass effect” can cause turbulence and vertical mixing on the leeward sides of islands subject to strong current flow (Glynn 1993). This process can lead to some cooling through vertical mixing and localized upwelling of deeper cooler waters; yet, even at consistently high temperatures (no upwelling), increased flow rates alone may confer some protection from bleaching.

Nakamura & van Woesik (2001) empirically tested the hypothesis that – since the photoinhibition phenomenon that accompanies bleaching involves the accumulation of harmful oxygen radicals – high current speeds could actually prevent bleaching by inducing high-mass transfer of detrimental photosynthetic byproducts out of the colony. Under controlled conditions of constant temperature (30 ^{o}C or greater) and light (30% photosynthetically active radiation [PAR], or photon flux in the 400-700 nm range), *Acropora digitata* colonies under low-flow conditions (< 3 cm/s) suffered high bleaching mortality while colonies under high-flow conditions (50-70 cm/s) showed no bleaching effects (Nakamura & van Woesik 2001). Hence, high water-flow may prevent, through diffusion, excessive build-up of toxins within corals subjected to high sea surface temperatures and high irradiance. This can prevent bleaching or minimize mortality after bleaching.

Various field observations appear to support these conclusions. In the southern Seychelles, the channel into Alphonse atoll (where there is fast water flow) was relatively unscathed by the 1997-1998 bleaching event, with abundant healthy massive, branching and fire corals unaffected (C. Bradshaw, personal observation). In Indonesia, corals in southern communities where currents are strong – such as Komodo National Park – did not bleach, while those in sheltered northern reefs exhibited bleaching (L. Pet, personal observation). It must be noted that for all of these examples of the moderating effect of water movement on bleaching, it can be difficult to distinguish between the effect of water movement and the potentially confounding factor of upwelling in driving these patterns. Further studies and field data are needed to determine the frequency and extent of water movement's protective effect across species and sites, including improved oceanographic information for all oceans so that the influences of flow and localized upwelling can be clearly distinguished.

Physical Factors that Decrease Light Stress

Light quality and quantity are important secondary factors that work in combination with temperature to exacerbate bleaching (Hoegh-Guldberg 1999). The role of PAR (400-700 nm wavelengths) in amplifying photoinhibition triggered by heat stress – with consequent exacerbation of bleaching – has been demonstrated experimentally (Hoegh-Guldberg 1999 and references therein). While more precise wavelength studies are needed, there is growing evidence for an important role of ultraviolet radiation (UV-R; 280-400 nm wavelengths) in bleaching as well (e.g., Gleason & Wellington 1993). Lesser & Lewis (1996) provide an UV-R action spectrum for photosynthesis inhibition in *Pocillopora damicornis*, Lesser et al. (1990) show that PAR and UV-R independently increase the activities of enzymes responsible for detoxifying active forms of oxygen, and Drollet et al. (1994, 1995) provide field evidence that distinguishes a role of UV-R in a bleaching event in Tahiti (see also Shick et al. 1996 for a balanced discussion on UV-R).

In the case of both PAR and UV-R, shading of corals, or parts of corals, may moderate the severity of bleaching during ENSO events. Examples include observations of less severe bleaching in fissures (compared to summits) of massive corals and on partially shaded sides of colonies in Panama (Glynn 1984), the Galapagos Islands (Robinson 1985), and Jamaica (Glynn & D'Croz 1990). In the Rock Islands of Palau, the same species of *Acropora* and *Porites* that were severely bleached and dead in some locations were alive and healthy in appearance in deeply shaded parts of the same reef (R. V. Salm, personal observation).

Protection from solar radiation can also occur in the form of light attenuation through scattering by suspended particulate matter (turbidity) or absorption by chromophoric dissolved organic matter (CDOM) in the water column. Goreau et al. (2000) reported lower bleaching mortality in very turbid waters in the Gulf of Kutch, Southwestern Sri Lanka, Mahe, and inside the lagoon of Alphonse atoll (Seychelles). In the Florida Keys, CDOM makes a major contribution to the ocean color signal in the short wavelength visible region (Anderson et al. 2001). Since CDOM absorbs UV radiation much more strongly than visible radiation and generally much more strongly than particulates (phytoplankton and detritus), these data indicate that CDOM may play an important role in controlling UV penetration in coastal habitats for coral assemblages.

Light attenuation from particulate matter and absorption by CDOM can contribute to an inverse relationship between irradiance and depth. Mumby et al. (2001*b*) found an inverse depth-mortality relationship for *Porites* in French Polynesia, presumably from exponential attenuation of solar radiation with increasing depth. Yet, this pattern of protection from bleaching with depth does not always hold true. Spencer et al. (2000) found the opposite pattern at sites in the Southern Seychelles, where deep corals bleached earlier and more extensively than their shallow-water counterparts. The reasons for these differing results and the role, if any, of solar irradiance in contributing to these patterns remains to be determined.

Finally, cloud cover can also afford protection from solar radiation. In Tahiti, there was no mass bleaching event in 1998, despite severe bleaching elsewhere in French Polynesia. The year 1998 was the cloudiest summer on record, and bleaching did not occur despite high sea surface temperatures similar to previous years when bleaching did occur. In a model recently developed by Mumby et al. (2001*a*), bleaching was strongly predicted for 1998 based on sea surface temperatures and wind speed alone. “No bleaching” was accurately predicted only when cloud cover was included in the model as an additional parameter.

Factors that Correlate with Bleaching Tolerance

Another category of factors to consider are those that may favor pre-adaptation (physiological tolerance) of corals to resist coral bleaching due to the presence of regularly stressful environmental conditions. The history of exposure to high temperatures can influence the thermal tolerance of corals, and thus their resistance to bleaching (Jokiel & Coles 1990; Marshall & Baird 2000; Craig et al. 2001). Coles & Jokiel (1978) concluded that high acclimation temperatures might have increased survival of Hawaiian *Montipora verrucosa* during subsequent thermal stress. In other cases, the relationship between the temperature history of a reef site and bleaching response may be due to strong selection for tolerant genotypes. Podesta & Glynn (2001) recorded lower mortalities after the ENSO of 1997-1998 compared to that of 1982-1983 at the same sites in the Galapagos, attributing the difference to strong selection for host/symbiont combinations more resistant to high temperatures.

Various other researchers have also speculated on the relationship between the temperature history of a reef site and bleaching response. P. A. Marshall & A. H. Baird (personal observation) have noted that small confined areas such as Geoffrey Bay (Great Barrier Reef) are subject to regular heating events during summer low tides, when water can “pond” over the wide and shallow upper reef -- and this type of phenomenon has been invoked to explain the lower bleaching susceptibility that has been recorded for corals from some inner reefs and lagoons relative to conspecifics from deeper waters (Hoeksema 1991). Similarly, reefs with emergent corals that were presumed to be tolerant of exposure to air as well as heat-stress – such as those on the reef flats in the Rock Islands of Palau (R. V. Salm, personal observation) and Chumbe Island in Tanzania (S. Riedmiller, personal observation) – suffered significantly less bleaching than corals down the reef slopes.

Where there are no data that directly indicate which coral communities are heat-stress tolerant, it may be possible to infer indirectly which assemblages in an area or region are likely to contain resistant genotypes, or phenotypes that can readily acclimatize to stressful conditions. In regions that are known to have experienced bleaching events in the past, broad size and frequency distributions, presence of large old corals, and large percentages of coral cover may be good indicators of potentially resistant assemblages. A team of researchers from the Australian Institute of Marine Science (AIMS) and the National Oceanic and Atmospheric Administration (NOAA) are currently exploring methods for cross-referencing the locations of such assemblages with sea surface temperature data from direct observations or from NOAA satellite imagery (http://www.noaa.gov) to confirm whether assemblages at these sites were indeed exposed -- but nevertheless survived -- elevated sea temperatures (Done 2001).

A Consolidated List of Resistance Factors

We have identified four main categories of environmental determinants of resistance to coral bleaching: physical factors that reduce temperature stress, physical factors that enhance water movement, physical factors that reduce light stress, and factors that correlate with bleaching tolerance (Table 2). Each main category is broken down into various conditions that could be predictive of increased resistance to coral bleaching in specific areas. The presence of such local conditions is especially important where they coincide with – and moderate the effects of – large-scale ENSO events that could lead to mass bleaching in those areas.

Environmental Factors that Contribute to Coral Community Resilience

Resilience factors increase the capacity of coral reef communities to recover after mortality events. They operate by enhancing reef regeneration through recolonization and regrowth. Resilience factors fall into two broad categories. Intrinsic factors are those that are determined by the ecological characteristics of the particular coral reef community, such as the innate ability of different corals to produce larvae that will recruit successfully. Extrinsic factors are physical characteristics that render a reef more or less likely to receive larvae on prevailing currents, or that favor successful settlement and recruitment by those larvae.

Intrinsic Resilience Factors

Intrinsic resilience factors are biological or ecological characteristics of a community that can contribute to reef recovery after mortality events have occurred. Such characteristics include the capacity of remaining corals to produce abundant and/or robust larvae that will recruit successfully, and ecological interactions that can favor survivorship and growth once the recruits arrive. Done (2001) emphasized the importance of targeting for MPA inclusion strategic locations that maximize both strong and reliable recruitment of all species within the community and the likelihood that a portion of the propagules from those communities will effectively seed other areas. In this sense, communities with diverse populations of adult corals with high fertilization success and robust larvae (which will survive, recruit and grow successfully) can contribute to not only their own resilience, but to the resilience of other "downstream" communities as well.

Coral reef resilience also depends upon the non-coral biological components of reef communities -- i.e., a requisite variety of functional groups (Gunderson 2000). For example, Bythell et al. (2000) studied the effects of natural mortality events due to hurricanes at Buck Island Reef National Monument, St. Croix, US Virgin Islands; they attributed the resilience of their study reefs to the presence of sufficient grazing fish populations, which kept in check macroalgae that may otherwise have out-competed coral recruits for space (see also Rogers 2000). Thus, balanced communities of reef-dwelling organisms can play an important role in reef resilience by preparing or maintaining substrate for coral recruitment and growth after bleaching mortalities have occurred. In another example, McClanahan (2000) concluded that the triggerfish *Balistapus undulatus* is a keystone predator on Kenyan reefs because it controls the populations of its sea urchin prey. While they can benefit reefs by grazing on algae, urchins are also bioeroders that can contribute to excessive reef disintegration and destruction of coral recruits if their populations get too large. Hence, a balanced community of grazers and predators -- with sufficiently low abundance of bioeroders, corallivores, and diseases -- can be essential for maximal resilience of a coral reef that has suffered coral bleaching mortality.

Extrinsic Resilience Factors

Resilience factors that are extrinsic to the biological characteristics of the community include physical factors such as current patterns that may favor larval dispersal among sites, or physical conditions that enhance coral survivorship and growth. Some coral reef communities may be relatively more resilient than others based on their physical location with regard to oceanographic conditions. For most marine species, dispersal depends on currents and other processes (such as eddies) that deliver larvae to the settlement site and even concentrate them at certain locations (Dayton et al. 2000). Indeed, Roberts (1997) found that surface currents defined most of the dispersal patterns for a large number of species in the Caribbean. Thus, patterns of connectivity should be considered in the design of any MPA network that is meant to maximize resilience.

Besides oceanographic conditions at local or regional scales, other localized physical parameters at a site can also affect resilience. Physical conditions on a reef may be chronically affected by anthropogenic impacts such as pollution or destructive fishing practices, which negatively affect the ability of coral assemblages to recover from natural disasters (Hughes & Connell 1999). Hence, reefs with effective management in place -- such that direct anthropogenic stresses are kept to a minimum in that area -- are likely to have a higher resilience after bleaching episodes compared to reefs that are already suffering from multiple stressors (Salm & Coles 2001).

A Consolidated List of Resilience Factors

From the above information, we have developed a list of resilience factors that may contribute to coral reef recovery (Table 3). Factors are divided into two groups: biotic characteristics of coral communities (intrinsic factors) versus physical conditions of the site that are determined by external oceanography or management (extrinsic factors).

Reliability: Differences in Predictability and Persistence Among Factors

In cases where the goal is biodiversity conservation, coral reef areas that are likely to resist severe bleaching – or likely to have greatest resilience in the wake of bleaching events – due to the presence of one or more resistance or resilience factors should be managed carefully to safeguard them from other, direct anthropogenic stressors that managers have the ability to control at the source. The dual purpose of focusing on these areas is to maximize the conservation of biodiversity through protection of the most bleaching-resistant sites and to secure their role as sources of larvae to hasten recovery of down-current areas that are more susceptible to bleaching. Such down-current "sink" areas, especially those that have been identified to include resilience factors, should be managed to favor conditions for maximal larval recruitment and reef recovery.

In order to implement this strategy, we must first confirm which factors are more or less reliable (predictable *and* persistent) in their effects, compared to those that are unreliable and ephemeral. For example, shade beneath overhangs and below cliffs is predictable, while cloud cover is not, yet both can mitigate bleaching. The former should be targeted while the latter will be of less interest for management. Therefore, it is useful to categorize the various types of factors according to their degrees of reliability. "Reliability" refers to how predictable and persistent the presence of a factor is likely to be, including during and after ENSO events.

In Tables 2 and 3, we have proposed rankings of "High"or "Low" reliability for each factor. Note that the breakdown is not a rigid one. Some factors (e.g., turbidity or wind-driven upwelling) could potentially be categorized as having either Low or High reliability, depending on the particulars at a specific location. For each site at which managers are working, the reliability rankings will depend on the amount of scientific information available for that factor (e.g., connectivity) in that location (e.g., connectivity is understood much better in the Dry Tortugas of the Florida Keys than in many other parts of the world where data have not yet been collected).

Managers should identify and strategically target reliable factors relevant to their own reef areas for: (1) provision of special management and protection in existing MPAs and (2) determination of priority areas for establishment of additional MPAs. These latter sites would contribute to a network of interconnected sites that are mutually replenishing so that those that survive a major bleaching event are able to enhance the recruitment at and recovery of those that succumb. This corresponds closely to Nyström & Folke's (2001) concept of a matrix of coral reefs that contribute to the ability of component reefs to recover when faced with disturbance. However, before this information is applied extensively in a management setting, a targeted monitoring program should be implemented to determine whether the identified factors really are reliable *and* have a significant effect on bleaching resistance or resilience. So far, we have merely identified a list of factors of *potential* importance in determining bleaching resistance and resilience; the degree to which each one can have a significant impact, and the reliability of that impact, remains to be tested.

A Hypothesis-Driven Monitoring Program to Confirm Significance and Reliability

Ideally, we should be able to identify for managers which environmental factors: (1) have a significant positive effect on coral resistance and resilience during bleaching events *and* (2) are reliably present to protect corals from bleaching or to enhance recovery during/after warming events. The goal is to determine which factors should be focused on for management purposes. This requires strategic targeted monitoring in support of a hypothesis-driven monitoring program.

Because there is a complex array of factors that could be working concurrently, a broad, multi-site monitoring program is needed across multiple reef types and regions. A large and broad data set of this type is needed for robust analyses of which factors correlate most strongly with resistance and resilience. There may be some existing programs from which data can already be drawn, while others may need adapting for this type of hypothesis-driven approach. An added element of the analysis will be to consider management influences (e.g., MPA sites compared to control sites) to test the hypothesis that conditions at managed sites enhance survivability and recovery potential. A multivariate analysis should be the first step for identifying factors of greatest significance and reliability, with the potential for more sophisticated modeling in the future to better understand their operation and interactions.

A general approach for monitoring environmental factors for their effectiveness in mitigating coral bleaching damage is discussed in Coles (2001). Along with establishing baseline conditions and background variability, the program should include increased monitoring during the next bleaching event to carefully track coral condition, mortality, and recovery with respect to resistance and resilience factors. Techniques utilized should (1) be consistent and have sufficiently high resolution to detect significant changes in coral cover and composition; (2) collect data in a form that will be amenable to statistical analyses and storable in a variety of media; (3) consolidate data sets in a location that will make them accessible at a future date for comparison with existing conditions.

In summary, the goal is to monitor the condition of corals in areas where environmental factors of interest exist and in adjacent control sites where they have no influence, in order to determine whether there are indeed strong correlations between these factors and bleaching resistance and resilience, and whether the existence of MPA status in the area makes a difference. The intention is to utilize information from existing, in-place programs wherever possible, and to propose modifications that may make existing programs more amenable to evaluating the long-term effects of coral bleaching.

Conclusions

Salm et al.’s (2000) guidelines for MPA planning and management include the use of various categories of selection criteria (social, economic, ecological, regional, and pragmatic) for priority ordering of sites for MPA selection and zoning. Confirmation of environmental factors that afford protection from bleaching mortality may necessitate consideration of additional site selection criteria from a new category: survivability and resilience to climate change. That is, when evaluating existing MPAs or planning new ones, MPA managers should consider site selection criteria that will allow coral communities that are reliably influenced by one or more protective environmental factors to be carefully monitored and adaptively managed. Managers should also manage sites down current of these to enhance conditions for larval settlement and recovery of these dependent areas.

In the context of existing monitoring programs, managers could begin by surveying reefs both inside and outside of MPAs for the presence of reef areas with one or more reliable factors. They could then begin a process to afford higher levels of control at these locations, either by modifying management activities and zoning schemes in existing MPAs, or by establishing increased protection for newly-defined target areas. At the same time, the efficacy of these policies should be tested by including these sites in the suggested hypothesis-driven monitoring program to test the reliability and significance of the resistance and resilience factors. As data are collected and analyzed to determine the relative importance of different resistance and resilience factors -- as well the effectiveness of MPA management in further enhancing natural resistance and resilience -- it may be necessary to adjust management policies accordingly. This is consistent with an “adaptive management approach” (Gunderson 2000), in which policies are viewed as hypotheses, and management actions become treatments in an experimental sense. Such an approach would allow coral reef managers to begin acting immediately to conserve coral reef biodiversity based on what we already know about coral bleaching resistance and resilience, while also building into the process the capacity for future adjustment and refinement of management practices as new information becomes available.

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Wilkinson, C. 2000. Status of Coral Reefs of the World: 1998. Australian Institute of Marine Science, Queensland, Australia.

Table 1. Some examples of apparent resistance to bleaching-induced mortality during large-scale bleaching events, as reported by researchers in the field.

Location	Observation	Suggested Explanation	Source
Binh Thuan, Vietnam	rapid recovery from bleaching	upwelling	Chou (2000)
Indonesia, Malidives, Zanzibar	certain locations spared from severe bleaching	upwelling	Goreau et al. (2000)
Gulf of Oman	full recovery	upwelling	Salm et al. (1993)
Alphonse Atoll, Seychelles	area unscathed by bleaching event	rapid flow in channel	C. Bradshaw (personal observation)
Komodo Nat'l. Park, Indonesia	no bleaching	strong currents	L. Pet, (personal observation)
Panama, Galapagos Isl., Jamaica	less bleaching on colony fissures and sides	relatively less solar irradiance	Glynn (1984), Robinson (1985), Glynn & D'Croz (1990)
Gulf of Kutch, Seychelles	lower bleaching mortality	turbidity	Goreau et al. (2000)
Tahiti	no mass bleaching	cloud cover	Mumby et al. (2001*a*)
French Polynesia	inverse depth-mortality relationship	light attenuation	Mumby et al. (2001*b*)
Hawaii	increased survival of thermal stress	acclimation with repeated exposure	Coles & Jokiel (1978)
Galapagos Isl.	lower mortality during second bleaching event	strong selection for resistant host/ symbiont combinations	Podesta & Glynn (2001)
Palau, Tanzania	significantly less bleaching on emergent reef flats	tolerance due to regular exposure to air and heat	R. V. Salm (personal observation), R. Riedmiller (personal observation)

Table 2. A consolidated list of factors that may correlate with coral bleaching resistance.

Resistance Factor	Reliability[a]
Physical factors that reduce temperature stress	
Exchange (warm water replaced with cooler oceanic water)	High
Upwelling	High
Areas adjacent to deep water	High
Wind-driven mixing	Low
Physical factors that enhance water movement/flush toxins	
Fast currents (eddies, tidal and ocean currents, gyres)	High
Topography (peninsulas, points, narrow channels)	High
High wave energy	Low
Tidal range	Low
Wind	Low
Physical factors that decrease light stress	
Shade (high land profile, reef structural complexity)	High
Aspect relative to the sun	High
Slope	High
Turbidity	Low
Absorption/CDOM	Low
Cloud cover	Low
Factors that correlate with bleaching tolerance	
Temperature variability	High
Emergence at low tide	High
Indirect indicators of bleaching tolerance	
Broad size and species distributions	High
Areas of greatest remaining coral cover	High
History of corals surviving bleaching events	High

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[a] *"Reliability" refers to whether the factor is considered predictable and persistent in its operation (and thus of high value as a predictor of survivability).*

Table 3. A consolidated list of factors that may contribute to coral community resilience.

Resilience Factor	**Reliability**[a]
Intrinsic resilience factors	
Availability and abundance of local larvae	High
Recruitment success	High
Low abundance of bioeroders, corallivores, diseases	High
Diverse well-balanced community to prepare substratum for coral settlement (e.g., herbivorous fishes)	High
Extrinsic resilience factors	
Good potential for recovery because of effective management regime	High
Connectivity by currents (larval transport from other source reefs)	Low
Concentration of larval supply (e.g., concentration and settlement in eddies)	Low

[a] *"Reliability" refers to whether the factor is considered predictable and persistent in its operation (and thus of high value as a predictor of recovery potential).*