Coral Reef Resilience and Resistance to Bleaching

Gabriel D. Grimsditch & Rodney V. Salm

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Introduction

Coral reefs are vital ecosystems, providing a source of income, food and coastal protection for millions of people; and recent studies have shown that coral reef goods and services provide an annual net benefit of US$30 billion to economies worldwide (Cesar et al, 2003). Coral reefs are composed mainly of reef-building corals: colonial animals (polyps) that live symbiotically with the single-celled microalgae (zooxanthellae) in their body tissue and secrete a calcium carbonate skeleton. Coral reefs are formed by hundreds of thousands of these polyps and are found in warm, shallow, clear, low-nutrient tropical and sub-tropical waters, with optimum temperatures of 25-29ºC, although they exist in ranges from 18ºC (Florida) to 33ºC (Persian Gulf) (Buddemeier and Wilkinson, 1994). They are incredibly diverse, covering only 0.2% of the ocean's floor but containing 25% of its species and they are often dubbed the 'tropical rainforests of the oceans' (Roberts, 2003).

Unfortunately, coral reefs are also among the most vulnerable ecosystems in the world. Disturbances such as bleaching, fishing, pollution, waste disposal, coastal development, sedimentation, SCUBA diving, anchor damage, predator outbreaks, invasive species and epidemic diseases have all acted synergistically to degrade coral reef health and resilience. Today, an estimated 20% of coral reefs worldwide have been destroyed, while 24% are in imminent danger and a further 26% are under longer term danger of collapse (Wilkinson, 2004).

This paper synthesises much of the current scientific knowledge[1] on coral reef resistance and resilience to bleaching, a possible major effect of climate change. Following a brief overview of coral bleaching and what is meant by *resistance* and *resilience*, the paper highlights a variety of resistance and resilience factors and identifies some gaps in knowledge. It continues by providing an overview of some of the tools and strategies we can use to enhance coral reef resilience. Finally, it reviews current initiatives working on coral reef resilience and also identifying some possible future opportunities for research into the issue. A glossary of terms you may find unfamiliar can be found on page 38.

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[1] These sources were found at the University of Geneve Uni-Mail Library using the following search engines: Blackwell Synergy, Ingenta Select, Kluwer Online, Science Direct and Springer Link.
Sources were also found using Google searches of the internet.

Bleaching and other climate change-related threats to coral reefs

One predicted effect of climate change is increased coral bleaching (whitening), which is caused by the disruption of the symbiotic relationship between polyps and zooxanthellae resulting in the expulsion of zooxanthellae and loss of photosynthetic pigments. Stresses that can cause this include freshwater flooding, pollution, sedimentation, disease and, most importantly, changes in light and temperature. If stresses continue for long enough, corals and whole reefs can suffer reduced fecundity and growth rates, and eventually even mortality. Once sections of the coral reef die they become vulnerable to further structural degradation by algal overgrowth and bioerosion. Overall, though, the bleaching phenomenon is extremely patchy and can vary greatly according to location, environmental conditions, season or species composition. (Douglas, 2003).

Sea Surface Temperature & UV-radiation

Coral reefs are especially vulnerable to predicted climate change because they bleach rapidly and dramatically in response to increased Sea Surface Temperatures (SSTs). Corals live in environments that are close to their thermal threshold (the upper temperature limit for life), and even temperature increases of 1 or 2ºC above average over a sustained period of time (i.e. a month) can cause mass bleaching (Hoegh-Guldberg, 1999). The potential severity of the predicted increases of 1-3ºC in SSTs by 2050 (Hoegh-Guldberg, 1999) and 1.4-5.8ºC in Earth surface temperatures by 2100 (See Fig. 2- IPCC, 2001) thus becomes apparent.

Fig 1. Fully and partially bleached corals on the Great Barrier Reef.

Photo: Ray Berkelmans, Australian Institute of Marine Science

Furthermore, excessive UV-radiation acts synergistically with increased SSTs to exacerbate bleaching by producing harmful oxygen radicals (Lesser and Lewis, 1996) and causing mortality.

Large-scale bleaching events have been recorded with higher frequency since the 1980s and are linked to El Niño Southern Oscillation (ENSO) events. During the 1997/1998 ENSO, the most severe global bleaching event ever recorded occurred when bleaching occurred in over 50 countries. The Western Indian Ocean was worst affected, with 30% regional mortality (Obura, 2005). As temperatures continue to increase, events such as this could become more frequent and 'climate change may now be the single greatest threat to coral reefs worldwide' (West and Salm, 2003). Hoegh-Guldberg (1999) even predicted that mass bleaching could become an annual occurrence by 2020 in Southeast Asia and the Caribbean, by 2030 on the Great Barrier Reef and by 2040 in the central Pacific.

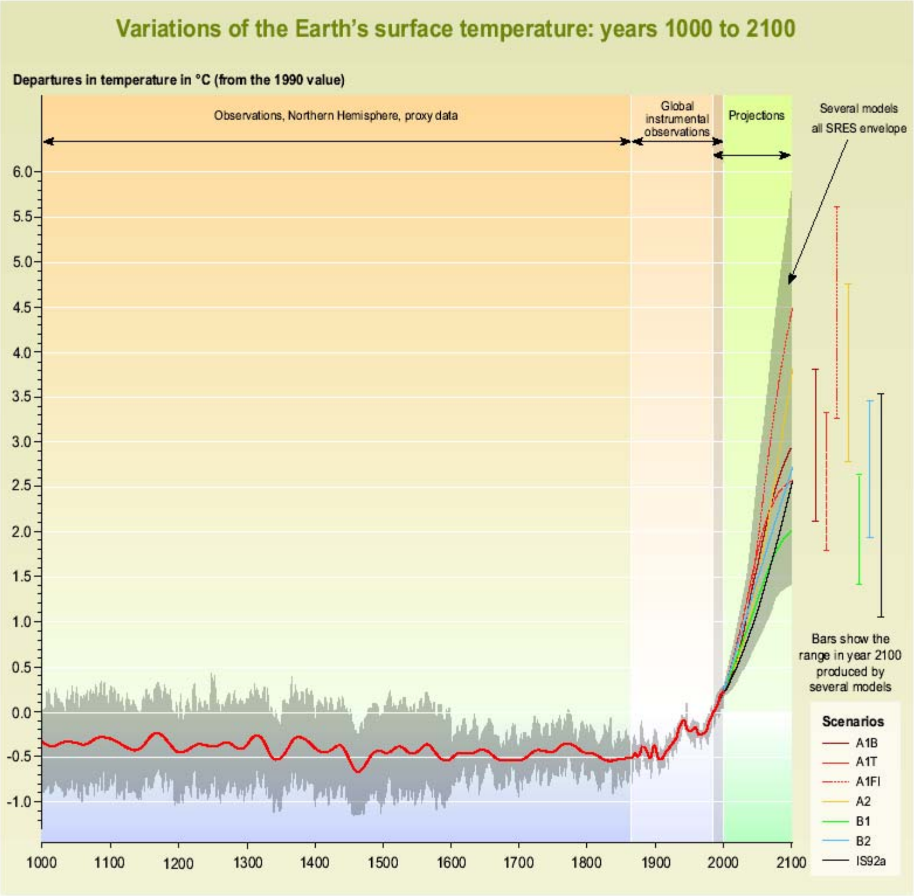

Fig 2. IPCC graph showing variations of the Earth's surface temperature, years 1000-2100. ©IPCC

Changes in seawater chemistry

As well as higher SSTs, the increase in the concentration of atmospheric CO_2 poses a threat to coral reefs by causing changes in global seawater chemistry; decreasing the concentration of carbonate ions and thus leading to decreases in coral calcification rates, growth rates and structural strength:

> Seawater absorbs CO_2 to produce carbonic acid (H_2CO_3), bicarbonate (HCO_3^-) and carbonate ions (CO_3^{2-}) with the following chemical reactions:
>
> $$H_2O + CO_2 = H_2CO_3$$
> $$H_2CO_3 = H^+ + HCO_3^-$$
> $$HCO_3^- = H^+ + CO_3^{2-}$$
>
> Carbonate ions are essential for calcification: $Ca^{2+} + CO_3^{2-} = CaCO_3$
>
> However, increases in atmospheric CO_2 levels lead to increases in the concentration of carbonic acid and bicarbonate ions, causing a decrease in the concentration of carbonate ions and a resultant reduction in calcification rates.
>
> This means that increases in CO_2 can cause decreases in the growth rates of corals (and other calcareous organisms) and weaken their skeletons. Their ability to compete for space on the reef is reduced and they become more susceptible to breakage and bio-erosion. If calcium carbonate removal exceeds the calcification rate, reefs can shrink in size (e.g. the Galapagos Islands). (Buddemeier et al, 2004)

However, the threat of climate change to calcification has been questioned by recent studies (see page 35, *Could climate change be positive for coral reef growth?*)

Rising sea levels

A further climate change-related threat to coral reefs comes from the predicted rise in sea levels. Normally coral reef growth can keep up with rising sea levels, but with projected rises of 1 to 9 mm/year (IPCC, 2001) some coral reefs may 'drown' in the future because of a lack of light as increased water volumes above the coral reefs reduce the light levels reaching them. However, it is expected that growth rates of most coral reefs will keep up with predicted sea level rises, and a more likely threat from sea level rise is increased sedimentation due to shore erosion (Buddemeier et al, 2004).

Natural resistance and resilience

Overall, the mitigation of negative effects due to climate change and other disturbances is of paramount importance. This paper will focus on coral bleaching, and will now discuss natural resistance and resilience exhibited by coral reefs to combat disturbance:

Resistance
The ability of an ecosystem to withstand disturbance without undergoing a phase shift or losing neither structure nor function (Odum, 1989). For example a coral reef's ability to withstand bleaching and mortality.

Resilience
The ability of a system to absorb or recover from disturbance and change, while maintaining its functions and services (Adapted from Carpenter et al, 2001). For example a coral reef's ability to recover from a bleaching event.

Because coral reefs exist in tropical latitudes within 30º of the equator in relatively constant environments with little seasonal cycling, it could be assumed that they are not highly resilient to environmental fluctuations. However, on a geological timescale they are among the most persistent ecosystems on Earth, having existed since the Paleozoic Era (543-248 million years ago). Some extant coral reef species have existed for the past 1-10 million years and have thus survived glacial-interglacial climate oscillations. Today, coral reef resilience is threatened by human-induced climate change that is predicted to lead to global temperatures that have not occurred since the Pliocene Era (5.3-1.8 million years ago) when coral reef species composition was significantly different (McClanahan et al, 2002).

The existence of coral reefs today is threatened because large disturbances can cause relatively quick phase shifts between ecological states of equilibrium of coral reefs when certain tolerance thresholds are crossed (Nyström et al, 2000). For example, in the Caribbean a major phase shift from coral- to macroalgae-dominated reefs has occurred since the 1980s due to the over-fishing of keystone herbivorous fish and the anthropogenic addition of nutrients to the seawater (Knowlton, 1992). Once such a phase shift does occur, it is extremely difficult to reverse it, so it is best for coral reefs to either **resist** bleaching in the first place or quickly recover from it through critical **resilience** factors.

This paper will first describe some important *resistance factors*:

1. Acclimatisation
2. The Adaptive Bleaching Hypothesis
3. Zooxanthellae Clades
4. Coral Morphology
5. Upwelling
6. Currents
7. Shading and Screening

Then some critical *resilience factors*:

1. Reproduction and Connectivity
2. Species and Functional Diversity
3. Shifting Geographic Ranges

And finally some *tools and strategies for enhancing coral reef resilience*:

1. Monitoring
2. Transplantation
3. Marine Protected Areas (MPAs)
4. Integrated Coastal Management (ICM)
5. Fisheries Management

Because of the variability and novelty of the bleaching phenomenon, the science behind it has many gaps. This paper will thus also discuss some *scientific gaps in knowledge* for each resilience and resistance factor. Finally, it will review some current initiatives working on coral reef resilience around the globe and identify some possible future opportunities for research. A short summary will be offered as a conclusion.

1.0 Resistance Factors

As defined above, bleaching resistance refers to the coral reef's ability to withstand bleaching and its associated mortality. We can further categorise resistance factors by those that contribute to bleaching *tolerance* and those that contribute to bleaching *avoidance*. Bleaching *tolerance* refers to actual physiological properties of corals that allow them not to bleach in stressful conditions. These include acclimatisation, evolutionary adaptation, different zooxanthellae clades and different coral morphologies. Bleaching *avoidance* refers to oceanographic and other environmental factors that create pockets of reduced or non-stressful conditions where corals are able to avoid severe bleaching. These include areas of local upwelling, strong currents or shading/screening (Salm et al, 2001; West and Salm, 2003; Obura, 2005).

1.1 Tolerance

1.1.1 Acclimatisation

The first tolerance factor is the ability of some corals to acclimatise to more stressful environmental conditions. Corals that are regularly exposed to stressful environmental conditions have, in some cases, been shown to acclimatise and exhibit physiological tolerance to elevated temperatures and UV-radiation that exceed normal thresholds. Corals have evolved temperature thresholds close to the average upper temperatures of their area, so thermal tolerance varies from region to region. For example, the average summer temperature on Lord Howe Island is 24°C compared to 36°C in the Arabian Gulf, so that similar corals in each location live under quite different temperature regimes and thus have different thermal tolerances (West and Salm, 2003).

Field evidence for acclimatisation comes from Brown et al.'s (2000) observations of *Goniastrea aspera* in Phuket, Thailand. During a bleaching event, *G. aspera* colonies bleached only on their east-facing surfaces despite almost identical conditions on either side at that time. It was shown that west-facing surfaces were subjected to higher levels of UV-radiation earlier in the year and thus became acclimatised and more resistant to bleaching.

Fig 3. Coral exposed at low tide in Guam.
Photo: Andrew Porter

Similarly, small confined areas that are regularly heated during low tides often show higher bleaching tolerance. This is probably why corals in inner reefs, lagoons and emergent (above water) corals are often more tolerant of elevated temperatures than corals further down the reef slope (West and Salm, 2003).

In areas that have suffered past bleaching events, large corals and high coral cover should be good indicators of resistant assemblages. A team of researchers from the Australian Institute of Marine Science (AIMS) and the National Oceanic and Atmospheric Administration (NOAA) is currently exploring methods to check such assemblages against SST data to determine whether they have survived high temperatures and thus have higher thermal tolerance thresholds than adjacent assemblages (West and Salm, 2003).

1.1.2 The Adaptive Bleaching Hypothesis

Another tolerance factor is the possible evolutionary adaptation of corals to elevated temperatures through bleaching. The Adaptive Bleaching Hypothesis proposed by Buddemeier and Fautin (1993) postulates that corals expel their zooxanthellae during a bleaching event in order to replace them with more resistant strains afterwards. Coral bleaching is thus seen as an evolutionary mechanism to adapt to rising temperatures. However, this theory is not universally accepted and is the subject of debate.

Baker's (2001) experiment in San Blas, Panama supports the theory. Corals were reciprocally transplanted between different depths, and zooxanthellae communities were observed to recombine to more tolerant combinations as corals were transplanted upwards to more stressful temperature and radiation conditions. Furthermore, Baker et al. (2004) showed that zooxanthellae communities recombined to more tolerant combinations after bleaching events in the Arabian Gulf, Panama, Kenya and Mauritius. Baker (2001) concludes that bleaching is an 'ecological gamble that… sacrifices short-term benefits for long-term advantage'.

On the other hand, some experts are critical of the theory. It has been argued that the recombining of zooxanthellae communities does not necessarily prove an evolutionary response is taking place, but that this is rather a phenotypic acclimatisation. Hughes et al. (2003) point out that the relatively long life of corals (often up to 20 years) does not fit the hypothesis and that current thermal resistance evolved over a much longer timeframe than predicted future climate change. Baker's experiment itself has been criticised by Hoegh-Guldberg et al. (2002) for not taking into account the difference in recovery potential between the two depths, and because the molecular procedure used has not definitely been proven capable of detecting genotypic differences between zooxanthellae. More experimental and field evidence is needed before the theory can be verified.

Scientific gaps in knowledge

The Adaptive Bleaching Hypothesis thus remains controversial. Obura (2005) believes that 'it may not yet be possible to address the evolutionary claims and consequences of the Adaptive Bleaching Hypothesis'. Moreover, the exact mechanisms of coral acclimatisation remain largely a mystery, and further research is necessary in this field.

Key questions include:

a) 'How do zooxanthellae community shifts in coral populations occur?' (Lewis and Coffroth, 2004)

b) 'How long do these zooxanthellae community shifts last?' (Baker et al, 2004)

c) 'Is acclimatisation algal- (zooxanthellae) or host- (coral) based?' (Brown et al, 2002)

d) 'Could the manipulation of zooxanthellae be used to increase the bleaching resistance of coral reefs?' (Ware et al, 1996)

e) 'Could adaptation occur via natural selection in corals and zooxanthellae?' (CRC, 2005)

f) 'What are the thermal limits (maximum temperatures) that corals can acclimatise to?' (CRC, 2005)

An interesting avenue of research is the possible implantation of zooxanthellae into corals or their genetic modification to increase their thermal resistance. In fact, molecular techniques could become increasingly important in coral reef research. Other physiological features that could be used to increase bleaching resistance involve heat-shock proteins, oxidoreductase enzymes (Fang et al, 1997), microsporine-like amino acids and the coral surface micro-layer that absorbs UV radiation (Aas et al, 1998).

1.1.3 Zooxanthellae Clades

Zooxanthellae (dinoflagellate single-celled microalgae that live symbiotically in coral polyps – genus *Symbiodinium*) play a crucial role in bleaching tolerance. Many strains, or clades, of zooxanthellae have been identified, and different clades display varying thermal, and therefore bleaching, resistances. These zooxanthellae are introduced into coral polyps either through inheritance from progenitors or by capture from surrounding waters in a process that allows host-symbiont recombination (Lewis and Coffroth, 2004).

However, zooxanthellae communities are by no means consistently homogenous. For example, multi-clade communities of zooxanthellae have been shown to exist in Caribbean *Montastrea annularis* and *Montastrea faveolata* coral communities. The type of clade present has been shown to vary according to the level of UV-radiation affecting that section of the coral reef. In the example above, shallow, high-UV corals contain predominantly more-resistant A and B clades while deeper, low-UV corals contain mostly the less-resistant C clade. These zooxanthellae community gradients are present in many sites and can influence bleaching patterns (Rowan et al, 1997).

Other micro-algae that have been shown to protect corals from bleaching are the endolithic algae (genus *Ostreobium*) living in some corals' skeletons. These algae can shield a coral against UV-radiation (Shashar et al, 1997), or can increase the survival chances of a bleached coral until the zooxanthellae population is restored, as shown by Fine and Loya (2002) in the Mediterranean coral *Oculina patagonica*.

1.1.4 Coral Morphology

As well as different zooxanthellae clades, different species and morphologies of coral have varying tolerances to bleaching. Species-specific responses to bleaching have been observed all over the world as described for Kenya by Obura (2005).

Considering morphology, it has often been observed that fast-growing branching species (e.g. *Acropora*, *Seriatopora*, *Stylophora*, *Millepora* and *Pocillopora*) suffer higher bleaching mortality than slow-growing massive species (e.g. *Favites, Favia, Goniastrea, Astreopora* and *Turbinaria*) (Marshall and Baird, 2000; Floros et al, 2004; McClanahan et al, 2004). The exact causes of this phenomenon are not completely understood. It is possible that the higher respiration and metabolism of protein in slow-growing corals allows harmful oxygen radicals to be eliminated more quickly. Another possibility is that the thick tissue of slow-growing corals could offer better protection for zooxanthellae against UV-radiation. Whatever the reasons, as branching coral populations are reduced by bleaching a long-term global shift from branching to massive corals and consequent loss of coral diversity is widely predicted (Loya et al, 2001).

Different coral morphologies display varying resistance to bleaching.
Fig 4. Branching *Pocillopora* corals off Seychelles. Branching corals are often more susceptible to bleaching.
Photo: ©Khaled bin Sultan, Living Oceans Foundation.

Fig 5. Massive Australian brain coral (*Goniastrea australensis*). Massive corals are often more tolerant to bleaching.
Photo: ©Great Barrier Reef Marine Park Authority

Scientific gaps in knowledge

More research is needed into the hypotheses surrounding the differences in resistance mechanisms of massive compared to branching corals. Furthermore, the implications of the predicted community shifts and loss of diversity remain unknown, and more research is needed into the possible socio-economic effects of such a shift on fisheries, tourism, coastal protection and ecosystem resilience. The overall economic cost of the 1998 bleaching event on tourism, shoreline protection and fisheries in the Indian Ocean is estimated to be between US$608 and 8026 million, and the great variation in those figures highlights the uncertainty and need for research (Cesar et al, 2002). Moreover, the incidence and rate of community shifts must be monitored to determine whether they are happening on a wide scale and to ascertain general trends. The causes of such shifts must be further investigated, as well as the cases where global trends are reversed, for example the 100% mortality of slow-growing *Agaricia tenuifolia* in Belize when branching *Acropora* were among the last to bleach (Aronson et al, 2002).

1.2 Avoidance

1.2.1 Local Upwelling

The first coral bleaching avoidance factor we shall discuss is upwelling. NOAA (2005) defines upwelling as: 'the process by which warm, less-dense surface water is drawn away from a shore by offshore currents and replaced by cold, denser water brought up from the subsurface'.

Large-scale upwelling over an area of hundreds of square kilometres hinders the development of coral reefs (e.g. in the tropical eastern Pacific; Glynn and D'Croz, 1990), but small-scale, local upwelling over an area of tens to hundreds of square metres can protect coral reefs against bleaching by reducing SST's or creating fluctuating thermal environments that induce corals to build thermal resistance over time. Examples of protection against bleaching by upwelling come from coral reefs in Binh Thuan, Vietnam and Sodwana Bay, South Africa (Riegl and Piller, 2003).

On the other hand, the opposite is sometimes true, as shown by an example from Panama. In the Gulf of Panama, corals were initially protected against bleaching for three months by seasonal upwelling while corals were bleached in the Gulf of Chiriqui, an area where upwelling does not occur. However, the subsequent ENSO event disrupted upwelling and corals in the Gulf of Panama ended up suffering higher bleaching mortality than those in the Gulf of Chiriqui because they had not become acclimatised to stress. This highlights the risk of depending on seasonal upwelling or other seasonal phenomena for the protection of coral reefs against bleaching (D'Croz and Maté, 2004).

Perhaps more reliable indicators of cooling that mitigate thermal stress and protect corals from bleaching are:

a) the mixing of deeper, cooler water with shallow, heated water because of tidal currents interacting with bathymetry and salinity, or
b) the proximity of coral reefs to deep water

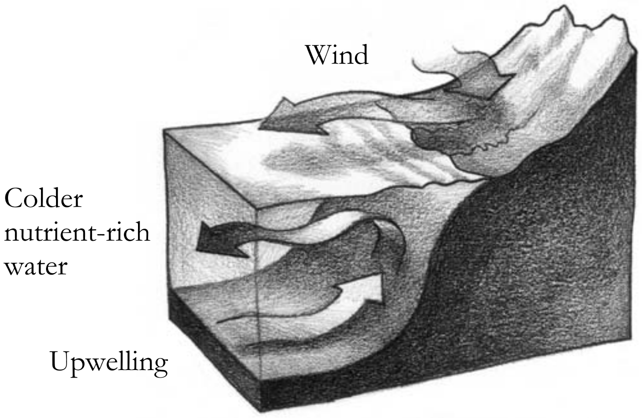

Fig 6. This general diagram shows how the process of upwelling brings colder, nutrient-rich water from the sea bed to the sea surface.
© Chris Jouan.

1.2.2 Currents

Another oceanographic phenomenon that allows corals to avoid bleaching is the fast water flow created by currents. Tidal currents and the associated fast water flow can protect corals against bleaching by removing harmful oxygen radicals. In fact, Nakamura and van Woesik (2001) showed that *Acropora digitata* colonies under faster flow conditions in the laboratory exhibited much lower bleaching mortality than colonies under slower flow conditions. A field example of this phenomenon comes from the channel into the Alphonse Atoll, Seychelles, where fast water flow protected corals in 1998 (West and Salm, 2003). Furthermore, fast water flow conditions can also improve coral reef resilience by preventing ecological phase shifts to macroalgae-dominated reefs by inhibiting algal settlement and allowing coral recruits to settle and grow (McClanahan et al, 2002).

Scientific gaps in knowledge

More field studies, more experiments, better modelling and especially better oceanographic data are necessary to distinguish and determine the roles and effectiveness of local upwellings and currents on coral reef resistance (West and Salm, 2003).

1.2.3 Shading and Screening

Finally, the shading of corals by clouds, high islands, rocks or other corals, or the screening of corals by suspended particulate matter, can protect them against UV-radiation and allow them to avoid bleaching in some cases. For example, shading by cloud cover allowed coral reefs in Tahiti in 1998 to avoid bleaching even though coral reefs in the rest of French Polynesia were severely bleached (Mumby et al, 2001). However, cloud cover may be too unreliable and impermanent to be considered a useful contributor to coral reef resistance. A more reliable avoidance factor is shading by high islands, emergent rocks or corals overhead. For example, in the Rock Islands of Palau, *Acropora* and *Porites* corals in more shaded parts of the reef survived a bleaching event better than those in more exposed parts of the reef (West and Salm, 2003). In fact, Riegl and Piller (2003) concluded that corals at moderate depths (20-30 metres) in the Red Sea and off South Africa could provide important refugia in the future and allow regeneration of coral communities from bleaching events.

In addition to shading, screening of UV-radiation through scattering of light by suspended particulate matter, as in turbid areas like the Gulf of Kutch (Goreau et al, 2000), or through light absorption by coloured dissolved organic matter, as in the Bahamas (Otis et al, 2004), can also protect corals from UV-radiation and allow them to avoid bleaching.

Fig. 7 Shaded corals off Hurghada, Egypt, Red Sea. Shading by overhanging structures can protect corals from bleaching.
Photo: Thomas Jundt

Scientific gaps in knowledge

Local variations in the relationship between coral depth and bleaching susceptibility emphasise the variable nature of the bleaching phenomenon and the need for more research into resistance mechanisms. For example, although deeper corals can be protected by shading or screening, in some sites deeper corals have been shown to bleach earlier and more intensely (e.g. Seychelles) (Spencer et al, 2000). Shallower corals could sometimes be more resistant because:

a) …they become acclimatised to UV-radiation (Brown et al, 2002)

b) …they contain more microsporine-like amino acids, which absorb UV-radiation. The concentration of microsporine-like amino acids in corals decreases with depth (Aas et al, 1998)

c) …of a depth-dependent zonation of zooxanthellae with more thermally-resistant zooxanthellae present in shallower corals (Rowan et al, 1997).

Micro-environments may also explain some differences in bleaching response. It is important to determine the exact factors determining the trends in coral depth versus bleaching susceptibility and to ascertain whether medium-depth corals could indeed provide crucial refugia during future bleaching events (Riegl and Piller, 2003).

2.0 Resilience Factors

Resilience refers to a coral reef's ability to absorb or recover from disturbance and change, while maintaining its functions and services (Carpenter et al, 2001). This requires some degree of ecological 'memory' within the system that stores information and makes it available for maintaining the system in a stable state. The remnants (or 'memory') of the disturbed ecosystem become growth points for its renewal and reorganisation, and this memory is present in biological functional groups that survive disturbances (Adger et al, 2005).

A system that tends to return to the same state even after major perturbations has high resilience, while one that shifts into another state has lower resilience. Certain factors can increase a coral reef's resilience. They can be categorised into *ecological* and *spatial* resilience factors, with the primary difference being the scale over which these factors apply. *Ecological* resilience factors are properties present within the spatial boundaries of the ecosystem. We shall discuss species and functional diversity in this context. *Spatial* resilience factors extend beyond ecosystem boundaries and include large-scale functions and processes. We shall discuss reproduction and connectivity, as well as shifting geographical ranges in this context (Obura, 2005).

2.1 Ecological Factors

2.1.1 Species and Functional Diversity

The main ecological factor that affects coral reef resilience to bleaching is a balanced biological and functional diversity (see Glossary) within the coral reef. It is essential to have a balanced ecological community with sufficient species interactions for coral reefs to recover from disturbances, and this applies not only to bleaching but to other disturbances as well (Nyström and Folke, 2001).

An especially important functional group for coral reef resilience is the grazing animal group, consisting of herbivorous fish and sea urchins among others. They enhance coral reef resilience by preventing phase shifts from coral-dominated reefs to algal-dominated reefs by keeping algal growth in check and allowing the settlement of slower-growing coral recruits rather than faster-growing algae. Their importance is highlighted in a classic example from Jamaica, where the overfishing of predators and competitors (herbivorous fish) of the black-spined sea urchin *Diadema antillarum* led to an explosion in its population, and thus to a reduction of the diversity within the herbivorous functional group. Grazing by *D. antillarum* was crucial to coral reef recovery after Hurricane Allen in 1981, but in 1983-1984 a pathogen killed off 95-99% of its population and a phase shift took place as macroalgae out-competed coral. The extent to which this phase shift is irreversible is still unclear (Nyström et al, 2000).

In addition to herbivores, other important functional groups that determine coral reef resilience are:

1) Scleractinian corals and coralline algae for building the structure

2) Mobile links (species that move between habitats increasing connectivity, e.g. fish often transport zooxanthellae between coral reefs)

3) Support areas for mobile links (e.g. seagrasses and mangroves as breeding grounds for fish)

4) Predators (these maintain a higher diversity of herbivores and control bioeroder populations)

5) Corallivores (these allow the dispersal of coral fragments and zooxanthellae)

6) Settling facilitators (bacteria, diatoms, coralline algae and worms that aid larval settlement)

7) A framework of dead coral and rubble (this provides habitat complexity and a substratum for recruits)

8) Herbivores (these graze algae, thus allowing coral recruits to settle and grow) (Nyström and Folke, 2001)

Functional diversity and ecological interactions between these functional groups can be severely compromised by anthropogenic disturbance. Consequently, ecosystem resilience, services and productivity can be reduced; resulting in even greater impacts of subsequent disturbances. If we also take into account that it is difficult for one species to replace another even ecologically-similar one in the functional framework of an ecosystem, we realise that the loss of even just a single species can often lead to ecological changes that are irreversible in the short-term (Nyström and Folke, 2001).

Fig 8. Parrotfish are keystone herbivores. Here we see a Queen parrotfish (*Scarus vetula*) in the Great Barrier Reef.
Photo: Chuck Savall

Scientific gaps in knowledge

Recognising the dynamic nature of coral reefs and their complexity, the identification of keystone species and functional groups and their subsequent protection becomes a challenge to coral reef managers worldwide. If keystone functional groups are identified and managed correctly, then not only is coral reef conservation improved, but the crucial coral reef services available to society can be better maintained (Nyström and Folke, 2001).

However, although functional diversity is considered crucial for coral reef resilience, it is not certain that species diversity is equally as important. McClanahan et al. (2002) state that 'species diversity may have the capacity to increase ecosystem resilience by ensuring that there is sufficient informational [species] redundancy to guard against the risks associated with environmental disturbance' but go on to say that 'evidence from coral reefs to support this hypothesis is at present ambiguous.' Therefore more work is needed on establishing the different contributions to coral reef resilience of both species and functional diversity.

2.2 Spatial factors

2.2.1 Reproduction and Connectivity

An important spatial factor for coral reef resilience is the connectivity between and within coral reefs. Coral's large populations and discharges of larvae create high genetic diversity that is crucial for resilience against disturbance (Nyström and Folke, 2001). These larvae are poor swimmers and need to be carried by water currents to settle on reefs, but they can travel thousands of kilometres this way, meaning that even remote coral reefs can be interconnected (Chia et al, 1984). Therefore upstream, larval-exporting 'source' reefs with diverse populations of healthy adult corals are crucial to maintain the genetic diversity and resilience of downstream, larval-importing 'sink' reefs. Unfortunately, large-scale mortality on a coral reef reduces its capacity to self-seed, so it is important that healthy corals produce abundant and robust larvae that reach the degraded reefs and then settle and grow. It is thus important to identify and protect source reefs and the ocean currents connecting them to sink reefs (Nyström et al, 2000).

An understanding of water movements and connectivity is essential for the creation of a coherent Marine Protected Area (MPA) network, and a well-planned and well-managed MPA network creates a larger and more diverse gene pool, thus enhancing coral reef resilience to disturbance. The timing of larval discharges, the strength and direction of currents, the distance between coral reefs, as well as the influence of climate all need to be taken into account in when designing such an MPA network.

Furthermore, the mode of reproduction of the corals also determines the range within which they can repopulate other reefs: asexually-reproducing corals (from coral fragments) disperse locally while sexually-reproducing corals (from larvae) can disperse over much larger distances (Nyström and Folke, 2001).

As well as good connectivity, appropriate substrates are also crucial for larval settlement. A framework of dead coral or surfaces of calcareous algae provide the best substrates for coral recruitment. Good substrates should be stable and surrounded by calm waters with salinity levels between 32‰ and 40‰, and they should have a good light source, a lack of macroalgae, appropriate grazing levels and limited sedimentation (Richmond, 1993). Encrusting coralline algae that aid settlement and growth of coral recruits also contribute to strong recruitment (Buddemeier et al, 1993). Because of the various substrate types, the varying connectivity, the varying environmental conditions and the different species involved, coral reef recovery from disturbances through recolonisation and regrowth can vary greatly spatially and temporally (Gleason, 1996).

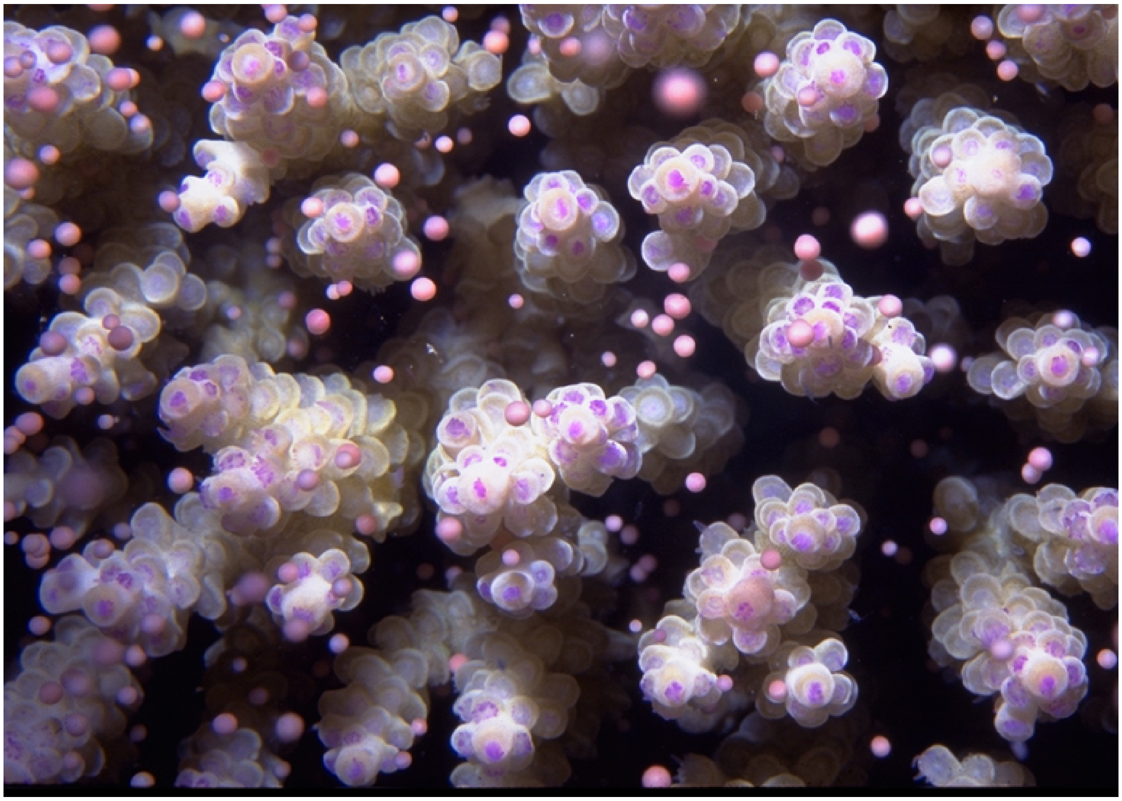

Fig 9. Purple hard coral (*Acropora cerealis*) releasing pink egg bundles in the Great Barrier Reef. Photo: Chuck Savall.

Scientific gaps in knowledge

The accurate mapping of coral reef connectivity is a growing need in MPA design and management. Roberts' (1997) work in the Caribbean is one such example of connectivity mapping, and more such studies are needed. To model connectivity, research must increase in scale and expand beyond the current focus on local monitoring and mapping. Nyström and Folke (2001) reflect this and state that 'coral reef management for conservation must expand beyond individual reefs towards cross-scale interactions within a matrix of reefs in dynamic seascapes and to an understanding of how the shifting mosaic of reefs contributes to ecosystem resilience'. Hughes et al. (2003) further criticise most coral reef research as 'parochial and short-term, providing little insight into global or longer-term changes'. Efforts should be co-ordinated on regional and even global scales to get a better view of the wider picture, intergenerational and genetic responses to climate change need to be investigated, and better oceanographic information for target regions should be acquired (Hughes et al, 2003).

Furthermore, the importance of local versus widespread larval dispersal needs to be investigated. As Nyström and Folke (2001) point out, 'the magnitude of variation in recruitment of corals at different spatio-temporal scales is poorly documented', although many studies have been made on the larval dispersal of other reef organisms. Some field studies show that reef organisms depend mainly on self-replenishment with retention of recruits from parental reefs or nearby reefs, so that large-scale connectivity by ocean currents is not the main factor (e.g. Ayre and Hughes, 2004; Barber et al, 2000; Cowen et al, 2000; Jones et al, 1999; Swearer et al, 1999). Ayre and Hughes (2004) even state that 'long-distance dispersal by corals to geographically isolated reefs cannot be achieved incrementally and is likely to be very rare'. On the other hand, other field studies show that larvae of reef organisms can disperse large distances and replenish populations on distant coral reefs (Domeier, 2004; Mora et al, 2003; Roberts, 1997; Veron, 1995). Thus the relationship of ocean currents and coral reproduction strategies and their influence on larval dispersal and recruitment patterns needs further investigation.

Concerning self-replenishment on coral reefs, more research is also needed for determining the minimum size of a coral reef for self-replenishment. Based on research in the Chagos Archipelago, Salm (1984) proposes a critical minimum size of 450 ha for coral reefs to be self-replenishing for all locally occurring species. Correctly addressing these gaps in knowledge would greatly improve the designation and management practices of MPA networks.

2.2.2 Shifting Geographic Ranges

Another interesting spatial resilience factor is the possibility that global changes in climate will promote the growth of coral reefs in marginal areas of the present range of coral reef distribution. There is evidence that during the Pleistocene (1.8 million to 10,000 years before present) and Holocene (10,000 years to present) eras many extant species shifted their ranges according to sea-level fluctuations (Buddemeier et al, 2004). For example, there is evidence that in the late Pleistocene coral reefs extended 500 km further south in western Australia than they do today (Hughes et al, 2003) and during the warmer Holocene coral reef species diversity is thought to have been double the present level in the currently marginal area of Tateyama, Japan (Buddemeier et al, 2004). Therefore, as the climate in present geographical ranges becomes less favourable, the diversity of coral reefs in presently marginal areas could increase. Nevertheless, Buddemeier et al. (2004) note that 'geographic shifts of coral reefs would not mitigate the ecological and economic problems caused by the loss of tropical reefs, but it would partly alleviate concerns about global biodiversity loss.'

However, conditions today are not as favourable for shifts in geographic ranges as they were in the past because

a) given the present high sea-level stand, projected sea-level rise is small compared to the rise that occurred during the Pleistocene when the large rise in sea-level aided shifts in geographic ranges

b) the areas where coral recruits attempt to settle today are hugely impacted by anthropogenic disturbances and are thus not always suitable for colonisation (Hughes et al, 2003).

Scientific gaps in knowledge

Overall, there seems to be little research into the possibility of climate-induced shifts in the geographic ranges of coral reef species. Sources that do mention the phenomenon usually examine past examples rather than future possibilities. Possible future research could involve identifying potential areas into which species could extend their ranges and the development of programmes to monitor such shifts. If the extension of geographic ranges becomes an apparent trend, appropriate management initiatives could be put in place in the new 'sink' areas. It could be possible to ensure optimal conditions for coral recruitment and growth in the new areas, or, conversely, to implement suitable management strategies if these coral reef species become problematic invasive species

3.0 Tools and Strategies for Enhancing Coral Reef Resilience

As coastal and marine environments become increasingly degraded due to anthropogenic activities, natural resilience of coral reefs will be weakened by impacts to their population structure, biodiversity and functional diversity. To combat this decline, certain management *tools* and *strategies* can be employed in order to attempt to enhance coral reef resilience. We refer to management tools as specific methodologies or actions used to manage the environment and to management strategies as general plans for coral reef management that make use of different management tools. Two important *tools* we present are coral reef monitoring and coral transplantation. Three important *strategies* we present are Marine Protected Areas, Integrated Coastal Management and fisheries management.

3.1 Tools

3.1.1 Monitoring

Ecological and socio-economic monitoring of coral reefs and their associated communities is a crucial management tool. Ecological monitoring focuses on the physical and biological parameters of coral reefs, while socio-economic monitoring aims to understand how people use and interact with coral reefs (Wilkinson et al, 2003).

Good monitoring programmes can be used to improve coral reef resilience by allowing the identification and protection of larval sources, connectivity patterns and representative and replicated habitat types, as well as allowing the effective management of other threats (The Nature Conservancy, 2004).

Fig 10. Monitoring is an essential tool for reef management.
Photo: Paul Marshall, Great Barrier Reef Marine Park Authority

For example, in a Global Environmental Facility-funded project in the Seychelles, monitoring proved to be an invaluable tool in improving coral reef resilience from a bleaching event. . It was especially useful for determining and mitigating threats to coral recruits from predators, for the identification of bleaching-resistant corals, for the identification of corals growing in upwelling areas and for the appropriate installation of moorings that reduced coral reef damage from boats (Engelhardt et al, 2003).

An intriguing possibility is the use of monitoring for predicting bleaching events. For example, Wooldridge and Done (2004) explored the use of a Bayesian belief network framework using remotely-sensed data, in-situ data and proxy variables from the Great Barrier Reef. They found that the best results for the prediction of coral bleaching came from the use of data concerning site heat stress (remotely sensed), acclimatisation temperatures (remotely sensed), cooling by tidal mixing (modelled) and the type of coral communities present (field data).

3.1.2 Transplantation

Another, more controversial, management tool that can be used to enhance coral reef resilience is coral transplantation, where juveniles from a healthy coral reef are introduced onto a degraded coral reef (Yap et al, 1998).

However, the effectiveness of this tool is the subject of debate. Some scientists believe that transplantation should only be used as a last resort if an area is not recruiting naturally. They claim natural recruits survive better than transplants and that in areas where natural recruitment is occurring, efforts should be directed at reducing stress (Edwards and Clark, 1998; Tamelander and Obura, 2002; Adger et al, 2005). Adger et al. (2005) believe that 'the upsurge in investment in artificial rehabilitation of reefs is misguided because it fails to reverse the root causes of regional-scale degradation' and is thus a 'quick fix' rather than a realistic long-term solution. Transplantation is also costly and limited in scope. It is probably best used to repair specific localised damage, such as areas of ship grounding or to 'house' reefs off tourist resorts, rather than as a tool for mitigating the impact of large-scale events, such as mass coral bleaching. However, if transplantation is absolutely necessary, Edwards and Clark (1998) advocate transplanting slow-growing massive corals rather than faster-growing branching corals for higher long-term success.

On the other hand, some scientists support the use of coral transplantations because natural recruitment is often limited and displays great inter-annual variation. They point out that transplantation of coral fragments can be beneficial by reducing the burden of reproductive success on source reefs (Soong and Chen, 2003; Epstein et al, 2003). Recent initiatives that encourage the use of coral transplantation and the creation of artificial coral reefs include the publication of the 'Manual for restoration and remediation of coral reefs' (Omori, 2004) by the Ministry of Environment of Japan, the creation of experimental coral gardens in Fiji (Lovell et al, 2004) and the establishment of the Reefball Foundation dedicated to restoring coral reefs artificially.

Fig 11. Artificial coral reefs at Royal Pahang Reef, Pulau Renggis, Tioman, Malaysia
Photo: Debby Ng

Nevertheless, the success of coral transplantations depends on many variable factors. Experiments by Oren and Benayahu (1997), Yap et al. (1998) and Yap (2004) have shown that responses to transplantation are highly site-specific and depend greatly on the depth of the transplants and local environmental conditions such as water quality, exposure, light levels or substrate stability. Furthermore, the success of coral transplantations could also be species-specific and dependent on the life history strategies of the particular species (Yap et al, 1992). The complications involved in these operations increase their costs and the chances of failure.

3.2 Strategies

3.2.1 Marine Protected Areas (MPAs)

Marine Protected Areas (MPAs) are the most widespread management strategy employed to enhance coastal ecosystem resilience and protect coral reefs. Although an MPA designation cannot usually directly protect a coral reef from bleaching, it can be used to improve coral reef resilience by protecting the coral reef from other anthropogenic disturbances. For example, anthropogenic impacts such as increased nutrient loads, pollution, diver and boat damage, sedimentation and destructive and over-fishing can be reduced. The reduction of these direct stresses contributes to resilience against bleaching by providing healthy corals and larval sources that are essential for coral reef recovery. Moreover, because bleaching events are usually patchy and do not result in 100% mortality of corals, it is important to determine the different responses of coral communities to bleaching events and the location of resistant pockets of coral communities. These resistant areas, or ‘refugia’, are a key component of overall coral reef resilience, and MPAs should protect such areas that have apparent low vulnerability to future bleaching. They should also protect areas with low anthropogenic disturbance, with suitable substrates for larval settlement and that will function as effective larval sources. Furthermore, they should ensure that local communities use coral reefs in a sustainable manner (Salm and West, 2003).

Ideally, an MPA should contain large and resistant coral colonies that produce large amounts of healthy larvae and display high biodiversity with fast- and slow-growing species being present. Furthermore, there should be minimal human disturbance, and preferably also upwelling water and winds and currents that flow past it from source reefs and towards sink reefs (Salm and West, 2003). Consequently, a good study of connectivity and currents is advisable when designing an interconnected and coherent network of MPAs. Nonetheless, even remote coral reefs that cannot be sources for widespread dispersal because they lack proximity to favourable currents are still be worth protecting because they could be sources for other local reefs (Westmacott et al, 2000). Furthermore, it is important to determine the reliability of favourable oceanographic phenomena, as processes such as upwelling can be seasonal or change from one year to the next (Done, 2001)

As well as high biodiversity and favourable oceanographic phenomena, MPAs should also include a wide variety of habitats and reef profiles in order to retain structural diversity. Structural features such as emergent substrates and back-reef lagoons are important because they often contain bleaching-resistant corals and provide nurseries for many fish species.

Fig 12. Managing MPAs involves working with the stakeholders on Marine Park enforcement.
Photo: Great Barrier Reef Marine Park Authority

Moreover, surrounding ecosystems such as seagrasses and mangroves should be protected because they contribute nutrients to the coral reefs, provide nurseries for many reef species and produce coloured dissolved organic matter (CDOMs), which can be important in screening harmful solar radiation and thus protecting corals against bleaching (Salm and West, 2003)

When designing MPAs, data concerning coral cover/age/exposure, sea surface temperatures, current strengths/directions, upwelling, water turbidity, fish movement/catches/spawning and tourism should be analysed. SST maps and connectivity maps (created by plotting currents and fish movement) can then be overlaid using Geographic Information Systems technology to determine the optimum shape and size of MPAs. Concerning MPA size, Salm and West (2003) favour fewer large MPAs over a greater number of smaller MPAs because larger coral reefs are more likely to be self-replenishing and to contain mixes of species communities at different stages of development and recovery. In addition, a coherent network of connected MPAs should display habitat replication and representativeness, so that a good cross-section of habitats is protected. In the Great Barrier Reef, this approach is guided by the notion of 'bioregionalisation', where the map is divided into areas occupied by 'groups of animals and plants… and physical features that are… distinct from [those of] surrounding areas' (Done, 2001).

Once target coral reefs have been identified, they should be protected from human disturbance as far as possible with management tools such as zoning schemes, monitoring schemes, boundaries and regulations. MPAs can be strict 'no-take zones' where no extractive activities may take place, or they can be broader 'multiple use protected areas' where several activities are managed and carried out in a sustainable manner. Multiple-use areas have the benefit of involving key stakeholders, but imply inherent risks and uncertainties involved with fisheries management. However, local awareness should be raised and local communities should be empowered to participate at the appropriate stages of the decision-making process as this often improves the success of MPAs (Done, 2001). MPA managers should also be properly trained and should have access to appropriate tools, equipment and management handbooks.

Examples of management handbooks

1. 'A reef manager's guide to coral bleaching' by Marshall and Schuttenberg (in press): GBRMPA
2. 'R^2- The Reef Resilience Toolkit CD-ROM' by TNC (2004)
3. 'How is your MPA doing?' by Pomeroy, Parks and Watson (2004): IUCN
4. 'Methods for ecological monitoring of coral reefs' by Hill and Wilkinson (2004): AIMS
5. 'Monitoring coral reef Marine Protected Areas' by Wilkinson, Green, Almany and Dionne (2003): AIMS
6. 'Enhancing reef survival in a changing climate: Additional Marine Protected Area guidelines to address coral bleaching' by Salm and West (2003): TNC
7. 'Buying time: A user's manual for building resistance and resilience to climate change on protected areas' by Hansen, Biringer and Hoffman (2003): WWF
8. 'Coral bleaching and Marine Protected Areas: Proceedings of the workshop on mitigating coral bleaching impact through MPA design' by Salm and Coles (2001): TNC
9. 'Coral reefs, mangroves and seagrasses: A sourcebook for managers' by Talbot and Wilkinson (2001): AIMS
10. 'Marine and Coastal Protected Areas: A guide for planners and managers' by Salm, Clarke and Siirila (2000): IUCN
11. 'Management of bleached and severely damaged coral reefs' by Westmacott, Teleki, Wells and West (2000): IUCN
12. 'Guidelines for Protected Areas' by Kelleher (1999): IUCN

3.2.2 Integrated Coastal Management (ICM)

An important management strategy that can complement an MPA network is Integrated Coastal Management (ICM). Coral reefs do not stand alone as ecosystems and are part of a larger seascape matrix, so the health of surrounding ecosystems such as seagrass beds, mangroves and adjacent watersheds is important for the health of coral reefs. Consequently, coral reef managers should take a holistic approach and integrate the management of coral reefs with the management of surrounding coastal ecosystems. ICM attempts to do this by treating the coastal zone as a single integrated ecosystem. A good ICM programme provides the framework for addressing issues such as coastal development, fisheries, tourism, land-based sources of pollution and sedimentation, waste disposal, agriculture, forestry, mining, gas and oil industries and shipping activities among others (Westmacott et al, 2000).

Fig 13. A marine park ranger installs a mooring buoy which will reduce anchor damage to corals in Bonaire Marine Park (Netherlands Antilles)
Photo: Dee Scarr

An example of a relatively effective ICM programme is the one in Belize, where management has evolved from a species-specific sectoral fisheries approach to the current ecosystem-wide approach of ICM and is moving towards a fully multi-sectoral strategy.

According to Gibson et al. (1998), the ICM strategy in Belize 'is likely to prove critical to successful long-term protection of the reef ecosystem' and 'provides a good model for sustainable coral reef management'.

3.2.3 Fisheries Management

The management of fisheries can play a crucial role in enhancing coral reef resilience. Coral mortality caused by bleaching can impact fisheries by affecting fishing yields, the composition of fish communities and the spatial distribution of fishing efforts. Conversely, destructive fishing practices such as blast- or poison-fishing can reduce coral reef resilience by decreasing coral cover or by depleting the populations of keystone functional groups (e.g. predators of crown-of-thorns starfish or herbivores that graze down algae and prepare the substrate for successful settlement and recruitment of coral larvae). Furthermore, over-fishing causes losses of biodiversity and functional diversity, and thus also reduces overall coral reef resilience (Westmacott et al, 2000).

Fisheries management can be aided by management actions such as the creation of no-take zones, the restriction of gear use, the imposition of fishing licences, the implementation of protective measures for key species, the implementation of legislation controlling destructive fishing techniques, the monitoring of catch compositions, the development of alternative livelihoods, and the regulation of the harvest of organisms for the curio and aquarium trades (Westmacott et al, 2000).

Fig 14. Excessive collection of marine organisms can lead to depletion and even extinction of local populations.
Photo: Jan Post

Today, the Great Barrier Reef is widely regarded as a model example of fisheries management with no-take areas totalling 33% (MPA News, 2004). Moreover, in the past some traditional management methods have also proved effective. For example, the Mijkenda people of East Africa had spiritual no-take zones and a territorial fishing system based on fees (McClanahan et al, 2002). Overall, no matter which approach is used, it is crucial that fishing practices be regulated in order to avoid the problems associated with destructive fishing and over-fishing.

4.0 Current activities and future opportunities

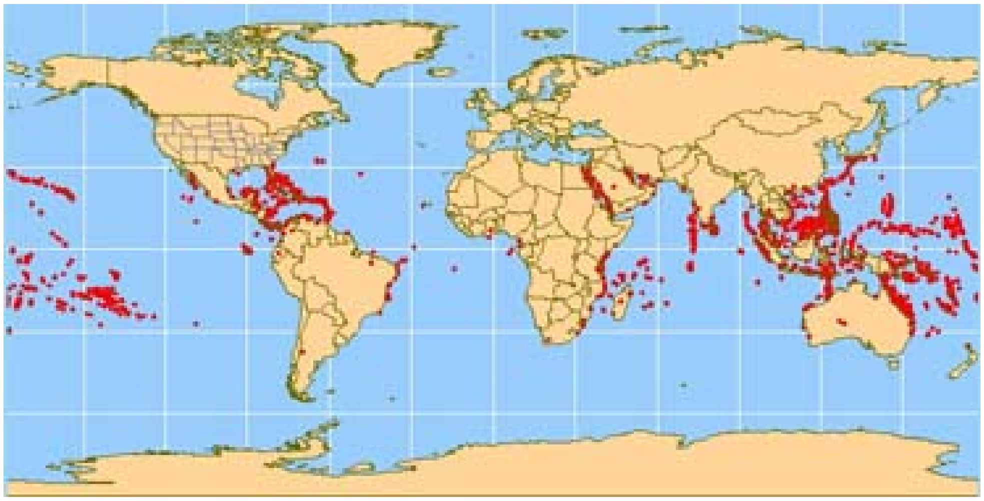

Fig 15. Major coral reef sites are seen as red dots on this world map. Most of the reefs, with a few exceptions are found in tropical and subtropical waters between 30° north and 30° south latitudes.
Courtesy of NOAA's Coral Reef Information System.

Mass coral reef bleaching on a global scale is a relatively new phenomenon, and its science is therefore in the developing stages. Several organisations around the world are investigating the resilience and resistance capacities of coral reefs to bleaching, and there is a need to co-ordinate information, knowledge and efforts on global and regional scales. In response to this growing need to co-ordinate efforts, programmes such as the Resilience Alliance, the IUCN Working Group on Tropical Marine Ecosystems, the Resilience Partnership, the Global Coral Reef Monitoring Network (GCRMN), the Global Environmental Facility Targeted Research Group (GEF-TRG), the Australian Research Council Centre for Excellence at the James Cook University (ARC-JCU), Coral Reef Degradation in the Indian Ocean (CORDIO), the Great Barrier Reef Marine Park Authority Climate Change Response Programme (GBRMPA-CCRP) and the Florida Reef Resilience Programme (FRRP), among others, have been initiated:

1) The Resilience Alliance was established in 1999 and is a research organisation of scientists and practitioners from many disciplines who collaborate to explore the dynamics of social-ecological systems. It thus has a broad focus that goes beyond coral reef resilience (Resilience Alliance, 2002). www.resalliance.org

2) The IUCN Working Group on Tropical Marine Ecosystems was formed in 2005 and includes some of the leading experts in the field of coral reef research. The first issue to be addressed by this group will be the issue of resilience, coral reefs and climate change, and the group aims to bridge gaps between the theoretical science of resilience and its practical management application in order to develop and implement tools that will improve the protection of coral reefs under the threat of climate change (IUCN, 2005). www.iucn.org

3) The above group works in close collaboration with the Resilience Partnership, which includes organisations such as The Nature Conservancy (TNC), World Wildlife Fund (WWF), The World Conservation Union (IUCN), Great Barrier Reef Marine Park Authority (GBRMPA), National Oceanic and Atmospheric Administration (NOAA) and Wildlife Conservation Society (WCS). This partnership focuses on incorporating resilience in the face of chronic, large-scale threats such as climate change into MPA selection, design and management, as well as into broader scale coastal management (TNC, 2005). http://nature.org

4) The GCRMN was created in 1995 and is an operating unit of the International Coral Reef Initiative (ICRI). It is the largest coral reef monitoring organisation in the world and acts as an umbrella organisation for the most important NGOs working with coral reefs as well as encompassing most countries with coral reefs. Monitoring data is accumulated in each region and entered into a specialised database compiled by ReefBase at The WorldFish Centre (GCRMN, 2004). www.gcrmn.org

5) The GEF-TRG established a global network of eminent coral reef scientists funded by a public sector alliance of the World Bank, Global Environmental Facility, NOAA, International Oceanographic Commission, Queensland government and University of Queensland. The group works to co-ordinate and target research in order to understand the science underlying the effects of climate change of coral reefs and how to manage the threat (GEF, 2005). www.gefcoral.org

6) The ARC-JCU focuses on innovative science for the sustainable management of coral reef biodiversity, and includes a programme on ‘Resilience of linked social-ecological systems’. Collectively, the ARC-JCU claims to create the world’s largest concentration of coral reef scientists (JCU, 2005). www.jcu.edu.au/school/mbiolaq/ccrbio

7) CORDIO is a collaborative operational programme under the ICRI and was created in 1999 to assess the widespread degradation of coral reefs throughout the Indian Ocean. Much of CORDIO's research focuses on mitigation of damage to coral reefs and on alternative livelihoods for people dependent on coral reefs that are being degraded due to climate change and other stress factors (CORDIO, 2005). www.cordio.org

8) The GBRMPA-CCRP is dedicated to understanding and reporting coral bleaching events and other climate change impacts on the Great Barrier Reef, as well as developing strategies to respond to this emerging threat. Furthermore, the GBRMPA is collaborating with NOAA, AIMS and IUCN to carry out research and produce guides for coral reef managers, and has been awarded an ARC grant to work on a programme on 'Management of coral reef resilience' (GBRMPA, 2005). www.gbrmpa.gov.au

9) The FRRP is a joint effort by the State of Florida, TNC, NOAA and GBRMPA. It is designed to improve our understanding of reef health in the region and to identify factors that influence the long-term resilience coral reefs in the area. Ultimately, the FRRP seeks to improve ecological conditions of Florida's reefs and economic sustainability by maximizing the benefits of naturally resilient reefs while seeking to improve the condition of those that are less resilient (FKNMS, 2005).
www.fknms.nos.noaa.gov/edu/soundingline/8th_ann_rept.pdf

In addition to these programmes, there are numerous other coral reef projects across the globe, and it is important for knowledge to be shared and co-ordinated in order to advance the field of coral reef resilience management and improve coral reef resilience to disturbances such as climate change. Future opportunities for these initiatives include filling the scientific gaps in knowledge outlined in this document, identifying further scientific gaps in knowledge, identifying geographical gaps in information and testing innovative management practices.

An important step would be to integrate theoretical resilience science principles into practical and meaningful managing strategies that are effective in the field and mitigate the climate change threat to coral reefs. As Obura (2005) points out, coral reef science should be '(a) specific enough to determine hypotheses on coral bleaching for scientific testing, and (b) general and heuristic enough to enable managers to develop interventions to mitigate bleaching impacts and design networks of MPAs'.

As well as the gaps in scientific knowledge already outlined in this paper, there are several other gaps in coral reef research that need to be addressed. For example, an interesting possibility is the analysis of data to attempt the mapping of the ecological and larger scale dynamics of coral bleaching due to climate change onto a framework of resilience theory (IUCN, 2005).

Other fields where further research could be conducted include the monitoring of resilience indicators, the economic valuation of coral reefs, sociological resilience, and the possibility of increased coral reef growth caused by warmer sea surface temperatures.

Monitoring

Furthermore, existing research and monitoring programmes should be strengthened and extended to areas that are currently not covered by such programmes. A recent study by Wilkinson (2004) and the GCRMN, 'Status of coral reefs of the world: 2004', focuses primarily on the state of health of coral reefs world-wide, but also discusses monitoring programmes reporting to and set up by the GCRMN. Using this report, it is possible to identify certain general geographical gaps in global coral reef monitoring.

Judging by the report, the largest gap in monitoring is the West Africa region where coral reefs are present: The Cape Verde islands and the Gulf of Guinea (Bioko, Príncipe, São Tomé, Annobón, Equatorial Guinea, Ivory Coast, Ghana, Senegal, Sierra Leone, Cameroon, Liberia). This region is not even mentioned in the report, yet the coral reefs are described by WWF (2005) as 'globally important coral reefs' and 'a top 10 global hotspot for coral communities' because of the high level of endemism in the area. Other countries identified by Wilkinson's (2004) report as not having GCRMN monitoring programmes are: Bangladesh and Pakistan in South Asia (Rajasuriya, 2004), and East Timor and Myanmar in Southeast Asia (Tun et al, 2004). Many other countries have monitoring programmes that are poor, inconsistent, lacking in funding or relatively new and have not produced substantial data (for example in Wallis and Futuna no GCRMN monitoring has yet been conducted; Vieux et al, 2004). These are also identified in the report. However, these conclusions do not take into account possible monitoring being undertaken by NGOs and governments that are not affiliated with GCRMN. It is thus possible that monitoring and research is being undertaken independently of GCRMN in these countries, and investigations into these areas could be useful.

An important step for research into resilience of coral reefs to climate change would be to develop resilience indicators and incorporate them into monitoring programmes. To address this issue, the Intergovernmental Oceanographic Commission (IOC), in partnership with GEF-TRG, created a Working Group on Coral Bleaching and Local Ecological Responses. One major output of the group will be a series of indicators and predictive tools applicable to coral bleaching. These include:

1) Molecular markers that distinguish heat stress from other stresses on coral reefs

2) Cellular markers that anticipate and monitor coral bleaching and recovery

3) Genetic markers that allow insight into resistance and resilience of reef-building corals

4) Ecological markers that allow the monitoring of impacts of coral bleaching

5) Scenario building of a more complete model of mechanisms that trigger mass coral bleaching in order to allow better prediction of climate change impacts on coral reefs and the effects on dependent societies.
(IOC, 2005)

Economic valuation

Another interesting field of research is the economic valuation of coral reefs, which can aid the sustainable management of coral reefs by showing the maximum benefits of coral reef uses to society, by quantifying and demonstrating to decision-makers the full costs of coral reef goods and services, and by providing better understanding of the stakes involved in multiple stakeholder problems. In fact, the International Coral Reef Action Network (ICRAN) encourages the use of economic valuation and cost-benefit analysis in economic and ecological research relating to coral reef threats (Chong et al, 2004). Concerning the 1998 bleaching event, the overall economic cost on tourism, shoreline protection and fisheries in the Indian Ocean has been estimated to be between US$608 and 8026 million (Cesar et al, 2002). This great variation in figures is partly due to our lack of knowledge of the effects of bleaching on fisheries and tourism, partly due to the uncertainties entailed in other socio-economic factors that influence fisheries and tourism apart from bleaching, and partly due to the lack of comprehensiveness in the field of coral reef economic valuation. ICRAN thus emphasises the need for standardised guidelines, methodologies, protocols and variables for economic valuation of coral reefs to be developed. Chong et al. (2004) analyse future research directions for economic valuation, policies and community participation concerning coral reefs. They call for research into:

1) equity distribution in order to understand livelihoods dependent on coral reefs

2) valuation of ecological functions in order to give a holistic view as to the worth of coral reefs

3) perceptions of the value of coral reefs by different stakeholders

4) the development of standard valuation techniques to allow comparisons between coral reefs

5) improving governance and legal systems for more efficient management of coral reefs

6) increasing awareness among coral reef users

These themes bring up the issues of *sociological resilience*, and it is important to remember that apart from the ecological resilience of the coral reefs themselves, it is essential to study and understand the resilience of the societies that depend on the coral reefs. Whether a society can recover from the effects of environmental adversities (e.g. a mass bleaching event) depends on factors such as, among others, robust governance, institutions for collective action, multilevel social networks, social capital, social 'memory', management frameworks and the opportunities for alternative livelihoods. Overall, the study of sociological resilience of coral reef-dependent societies is a crucial field for future research, and can be complementary and reinforce studies of coral reef ecological resilience (Adger et al, 2005).

Could climate change be positive for coral reef growth?

A further remarkable field of research is opened by the possibility that climate change could actually aid coral growth by increasing calcification. It is possible that increased SSTs facilitate the production of calcium carbonate by corals or zooxanthellae, and that this will counteract negative effects caused by increased CO_2 in oceanic surface waters. In fact, taking both CO_2 and temperature effects into account, it was calculated that the calcification rates of *Porites* corals would actually increase by 35% by the year 2100. Further research in this area could focus on whether increased temperatures affect coral or zooxanthellae calcification, and applying these new findings to coral reef and climate change models (McNeil, 2005).

Finally, the ultimate solution to protect coral reefs from mass bleaching would be to reduce the emissions of greenhouse gases and thus avoid, as far as possible, future climate change. However, this trend is governed by complex political and socio-economic factors that are generally out of the control of coral reef researchers. Nevertheless, continued research into climate change, its causes, consequences and the accurate prediction of geographic patterns and rates of change should be continued and enhanced.

Conclusion

Climate change poses a serious threat to the future health of coral reefs through the reduction of calcification rates and especially through the increased frequency and intensity of mass bleaching events. The 1998 global bleaching event was the worst ever recorded and has accelerated scientific research into the phenomenon. Through this research, it has been discovered that various factors interact to affect the resistance and resilience of coral reefs to bleaching.

The main resistance factors identified so far are:

1) Acclimatisation and adaptation of corals, including the adaptive bleaching hypothesis

2) Variation in thermal tolerances of zooxanthellae clades

3) Local water movement, e.g. upwelling that cools water or tidal currents that flush toxins

4) Shading or screening of corals that reduces the effects of harmful levels of UV-radiation

5) The morphology of a coral species

The main resilience factors identified so far are:

1) Connectivity between and within reefs

2) Species and functional diversity of a reef

3) Possible capacity to expand geographic ranges

To combat the predicted effects of climate change, several management tools and strategies can be implemented to enhance reef resilience.

The tools and strategies addressed in this paper are:

1) Monitoring programmes
2) Transplantation of corals
3) Coherent networks of well-selected and well-designed MPAs
4) Integrated Coastal Management
5) Fisheries management

However, the relative novelty of mass coral bleaching and its related science means that many gaps in knowledge still exist. Factors affecting resistance and resilience have recently been identified and, as Obura (2005) points out, 'the lack of a coherent set of hypotheses spanning all scales of the coral bleaching phenomenon is a barrier to the advancement of its study and management in a holistic sense.' Moreover, the bleaching phenomenon appears to be highly variable, largely unpredictable, and the factors causing it are complex.

Consequently, much controversy exists within the science of coral reefs and climate change, for example concerning the Adaptive Bleaching Hypothesis or the effectiveness and necessity of coral transplantations. Research into issues such as the mechanisms of adaptation and acclimatisation of corals, the importance of connectivity between reefs or the effects of local water movement on bleaching resistance, has answered but also created many questions. These and other scientific gaps in knowledge have been briefly addressed in this paper. For example, future opportunities in fields of research such as coral reef monitoring and economic valuation have been discussed. Furthermore, a brief overview of global initiatives working on coral reef resilience to climate change has been presented.

Overall, it is clear that climate change and coral reef health are inextricably linked, and that research should be coherent and co-ordinated in order to create more efficient solutions to the complex management challenges that will arise. There is thus clearly a need for coral reef science and management to be included in strategies that deal with the overall adaptation of human society to predicted climate change. With the increasing attention coral reef resilience is receiving from the marine science community, there is hope that this paradigm will enhance our general knowledge of ecosystem resilience to climate change, and that the lessons learnt studying it will be applicable on broader scales.

Glossary

Bayesian belief network: A model for representing uncertainties in knowledge (Wooldridge and Done, 2004).

Bioerosion: The erosion of substrate by means of biological procedures (Neumann, 1966).

Bioregion: An area where groups of animals and plants and physical features are distinct from those of surrounding areas. If one takes any slab of a bioregion, it should represent the biodiversity of assemblages, structure and environment as well as any other slab of the same bioregion (Done, 2001).

Calcification: A process by which the mineral calcium builds up in tissue, causing it to harden. Scleractinian corals produce aragonite ($CaCO_3$) skeletons via this process (Marshall, 1996).

Clade: A biological group of species that shares features inherited from a common ancestor (Houghton Mifflin, 2003).

Coloured Dissolved Organic Matter (CDOM): Also known as gelbstoff, it primarily consists of humic acids produced by the decomposition of plant litter and organically rich soils in coastal and upland areas. Levels can be augmented by fulvic acid produced by coral reefs, seaweed decomposition or industrial effluents (Keith et al, 2002). CDOM absorbs UV radiation and can protect coral reefs against bleaching (Otis et al, 2004).

Connectivity: The physical links between reefs, within reefs and between reefs and land (Andréfouët, 2002).

Coral bleaching: The disruption of the symbiotic relationship between polyps and zooxanthellae, resulting in the expulsion of zooxanthellae and loss of photosynthetic pigments (corals become white and weaken) (Douglas, 2003).

Coral reef: An erosion-resistant marine ridge or mound consisting chiefly of compacted coral together with algal material and biochemically deposited magnesium and calcium carbonates (Houghton Mifflin, 2003).

Coral surface microlayer: A protective layer of highly-productive mucus on the surface of corals. It is just millimetres thick but protects corals from UV-radiation (Aas et al, 1998).

Coralline algae: Algae species that form solid calcium carbonate accretions (NOAA, 2005).

Corallivore: An organism that eats coral (NOAA, 2005).

Diatom: A unicellular algae consisting of two interlocking silica valves (NOAA, 2005).

Ecological memory: After catastrophic change, remnants (memory) of the former system become growth points for renewal and reorganisation of the social-ecological system. Ecological memory is conferred by biological legacies that persist after disturbance, including mobile species and propagules that colonise and reorganise disturbed sites and refuges that support such legacies and mobile links (Adger et al, 2005).

Ecological phase shift: The shift of an ecosystem from one state of equilibrium to another due to disturbance (Nyström et al, 2001).

Ecological resilience: The ability of a system to absorb or recover from disturbance and change, while maintaining its functions and services (adapted from Carpenter et al, 2001).

Ecological resistance: The ability of an ecosystem to withstand disturbance without undergoing a phase shift or losing neither structure nor function (Odum, 1989).

Ecological state of equilibrium: The state in which the action of multiple forces produces a steady balance, resulting in no change over time (NOAA, 2005).

Ecosystem function: The process through which the constituent living and nonliving elements of ecosystems change and interact (ForestERA, 2005).

Ecosystem structure: The individuals and communities of plants and animals of which an ecosystem is composed, their age and spatial distribution, and the non-living natural resources present (APEX, 2004).

El Niño Southern Oscillation (ENSO): A disruption of the ocean-atmosphere system in the tropical Pacific having important consequences for weather around the globe. ENSO events can cause mass coral bleaching (NOAA, 2005).

Endemism: An endemic species has a distribution restricted to a particular area (NOAA, 2005).

Endolithic algae: Algae that burrow into calcareous rocks or corals (NOAA, 2005).

Fecundity: The potential reproductive capacity and productiveness of an organism or population (NOAA, 2005).

Functional diversity: The range of functions that are performed by organisms in a system (Gray, 1997).

Functional group: Groups of species with similar ecological roles/functions (Peterson, 1997).

Genotype: The genetic constitution of an individual or group (NOAA, 2005).

Geographic Information Systems (GIS): A computer system capable of assembling, storing, manipulating, and displaying geographically referenced information, i.e. data identified according to their locations. Practitioners also regard the total GIS as including operating personnel and the data that go into the system (USGS, 2005).

Global Environmental Facility (GEF): The GEF is an independent financial organization established in 1991 that provides grants to developing countries for projects that benefit the global environment and promote sustainable livelihoods in local communities (GEF, 2004).

Heat Shock Protein: Proteins present in the cells of all living organisms. They are induced when a cell is exposed to certain environmental stresses. Heat shock proteins are also present in cells under normal conditions, assisting in other cellular protein functions and behaviour (NOAA, 2005).

Holocene: An epoch of the Quaternary period dating from the end of the Pleistocene approximately 10,000 years ago until the present (NOAA, 2005).

Informational redundancy: See 'Species redundancy'.

In-situ data: Data associated with reference to measurements made at the actual location of the object or material measured, by contrast with remotely-sensed data, i.e., from space (PODAAC, 2005).

Keystone species: a species that plays a large or critical role in supporting the integrity of its ecological community. (Georgia Museum of Natural History, 2000)

Lagoon: A warm, shallow, quiet water body separated from the sea by a reef crest (NOAA, 2005)

Larvae: A sexually immature juvenile stage of an animal's life cycle (NOAA, 2005).

Life history strategy: The significant features of the life cycle through which an organism passes, with particular reference to strategies influencing survival and reproduction (USGS, 2005).

Light absorption: Matter converts light energy to internal heat or chemical energy, thus dissipating it (Petzold, 1972).

Light scattering: The direction of travel of light photons is changed so that they are dispersed and the light energy is decreased, although the wave length stays the same (Petzold, 1972).

Macroalgae: Multicellular algae large enough to be seen by the human eye (NOAA, 2005).

Mangrove: Halophytic (salt-loving) plants over 50 cm high that grow in tropical intertidal zones (NOAA, 2005).

Marine Protected Area (MPA): Area of the marine environment where cultural and natural resources are protected by federal, state, tribal or local laws or regulations (NOAA, 2005).

Microsporine-like amino acids: UV-absorbing compounds found in coral tissues. Thought to be produced by zooxanthellae (NOAA, 2005).

Mooring: An arrangement for securing a boat to a mooring buoy or a pier. Boats using moorings do not have to use traditional anchors, thus reducing damage to coral reefs (GBRMPA, 1996).

Morphology: The form and structure of organisms (NOAA, 2005).

No-Take Zone: An MPA that is completely (or seasonally) free of all extractive or non-extractive human uses that contribute impact (NOAA, 2005).

Oxidoreductase enzymes: Multiple enzymes (organic catalysts) that work together to quench harmful active oxygen (Lesser, 1997).

Oxygen radical: Highly reactive oxygen molecules that have lost an electron and thus stabilise themselves by 'stealing' an electron from a nearby molecule. Their high reactivity means they can cause cell damage (Houghton Mifflin, 2003).

Paleozoic Era: An era of geological time lasting from 543 to 248 million years ago (UCBMP, 2005).

Particulate: A very small solid suspended in water (NOAA, 2005).

Pathogen: An organism which causes a disease within another organism (NOAA, 2005).

Phase shift: See 'Ecological phase shift'.

Phenotype: The total characteristics of an individual resulting from interaction between its genotype (genetic constitution) and its environment (NOAA, 2005).

Photosynthesis: Process by which autotrophic chlorophyll-containing organisms manufacture their own energy sources (simple sugars) from the intracellular chemical reaction of carbon dioxide and water in the presence of sunlight and chlorophyll (NOAA, 2005).

Photosynthetic pigment: A pigment that efficiently absorbs light within the 400-700 nm range and is essential for photosynthesis (NOAA, 2005).

Pleistocene: An interval of the Quaternary period, from 1.8 million years before present to 10,000 years before present (NOAA, 2005).

Pliocene: An interval of the late Neogene period, from 5.3 to 1.8 million years before present (NOAA, 2005).

Polyp: An individual of a solitary cnidarian or one member of a cnidarian colony. Cnidarians are an animal phylum containing stony corals, anemones, sea fans, sea pens, hydroids and jellyfish (NOAA, 2005).

Proxy variable: In monitoring studies, a proxy variable is something that is probably not in itself of any great interest, but from which a variable of interest can be obtained. For examples, isotope ratios in coral skeletons are often used to determine environmental temperatures of the past. Wooldridge and Done (2004) used the highest 3-day summer SST's as a proxy variable for maximum heat stress for a site.

Recruit: New individuals entering a population, either sexually (e.g. coral larvae) or by immigration (NOAA, 2005).

Refugia: Regions that during climatic upheaval, biological stress or major population downsizings, still provide the essential elements of the species' niche for small subpopulations (Calvin, 2002). For example, shaded areas of coral reefs could provide refugia during bleaching events.

Remotely-sensed data: Data collected about an object or event without there being any physical contact with the object or event. Examples are satellite imaging and aerial photography (NOAA, 2005).

Resilience: See 'Ecological resilience'

Resistance: See 'Ecological resistance'

Scleractinia: An order of Cnidaria. Scleractinian corals produce calcareous skeletons with hexameral symmetry (NOAA, 2005).

Seagrass: Flowering plant found in marine or estuarine waters that tend to develop extensive underwater meadows (NOAA, 2005).

Sedimentation: The accumulation of soil and mineral particles washed into a water body, normally by erosion, which then settle on the bottom (Friedman and Friedman, 1994).

Sink reef: A downstream reef that imports larvae of corals and other reef-related organisms from upstream source reefs (Nyström and Folke, 2001).

Social memory: After catastrophic change, remnants (memory) of the former system become growth points for renewal and reorganisation of the social-ecological system. Social memory comes from the diversity of individuals and institutions that draw on reservoirs of practices, knowledge, values and worldviews and is crucial for preparing the system for change, building resilience, and for coping with surprises (Adger et al, 2005).

Source reef: An upstream reef that exports larvae of corals and other reef-related organisms to downstream sink reefs (Nyström and Folke, 2001).

Species redundancy: The presence of multiple species that play similar roles in ecosystem dynamics, thus enhancing ecosystem resilience (SER, 2004).

Substrate: The material making up the base upon which an organism lives or to which it is attached (NOAA, 2005).

Symbiosis: A relationship between two species of organisms in which both members benefit from the association (mutualism), or where only one member benefits but the other is not harmed (commensalism), or where one member benefits at the expense of the wellbeing of the other (parasitism). Polyps and zooxanthellae are mutually beneficial (NOAA, 2005).

Tidal mixing: Occurs when strong tidal currents mix the water column (Davis and Browne, 1997)

Transplantation: Management strategy where coral juveniles from a healthy reef are introduced onto a degraded reef (Yap et al, 1998).

Turbidity: Cloudy water, usually caused by the suspension of fine particles in the water column. The particles may be inorganic (e.g. silt) or organic (e.g. single-celled organisms) (NOAA, 2005).

Upwelling: The process by which warm, less-dense surface water is drawn away from a shore by offshore currents and replaced by cold, dense water brought up from the subsurface (NOAA, 2005).

Zooxanthellae: Dinoflagellates that live symbiotically (mutually beneficial) within a variety of invertebrate groups (e.g. coral polyps) (NOAA, 2005).

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