

A photograph of coral bleaching, showing white, skeletal coral structures against a dark blue background. The coral is mostly white and yellow, with some dark brown patches. The background is a deep blue, suggesting the ocean surface.

Coral Bleaching: The Synergistic Effects of Temperature and Photoinhibition

Tracey Saxby

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Tracey Saxby BSc BA

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Department of Botany

The University of Queensland

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1. Introduction

Coral reefs are highly productive ecosystems (Hughes 1994) formed primarily by hermatypic corals that precipitate a calcium carbonate skeleton, cemented together by coralline algae. These complex limestone structures provide an important habitat for a biologically diverse array of species (Guzmán and Guevara 1998). It has been suggested that the constant change brought about by intermediate levels of disturbance create biologically diverse communities in different stages of succession (Connell 1978; Hughes 1994; Brown 1997). Disturbance can be described as any relatively discrete event in space and time that removes organisms or otherwise disrupts the community by influencing the availability of space or food resources, or by changing the physical environment (Pickett and White 1985).

Coral reefs have evolved to cope with a variety of natural disturbances (Brown 1997) such as high energy storms or cyclones (Bourrouilh-Le Jan 1998), increased or decreased salinity (Davies *et al.* 1997; Berkelmans and Oliver 1999), sedimentation and turbidity (Jell and Flood 1978; Hubbard 1986), and aerial exposure. However, over the last few decades they have also been increasingly subjected to various anthropogenic impacts (Wilkinson 1993) including increased rates of sedimentation and eutrophication (Johannes 1975; Hallock *et al.* 1993), overfishing (Sebens 1994), mining and local impacts associated with tourism such as reef walking (Neil 1990) and boat anchoring (Brown 1997). Various combinations of all these destructive factors have altered reefs in all localities, with more than 11% of the world's reefs already lost due to human impacts (Wilkinson 2000). Recovery of a reef community is dependent upon the intensity and type of disturbance that caused the decline (Connell 1997; Connell *et al.* 1997).

Historically, reefs have recovered from natural disturbances, however recent evidence indicates that changes in community structure and composition have increased in scale and frequency, and recovery is frequently delayed (Glynn 1993; Hughes 1994). While natural disturbances play an important role in maintaining high levels of diversity within coral reef ecosystems, the addition of human-induced disturbances may have a detrimental effect on coral reefs. Increasing frequency and severity of human-induced disturbances may exceed the rate at which coral communities can recruit and successfully reproduce (Sebens 1994).

Coral bleaching is considered to be a typical response to extreme environmental conditions, (Yonge and Nicholls 1931; Hoegh-Guldberg and Smith 1989; Fang, *et al.* 1997; Jones *et al.* 1998) and has been observed in response to several different factors, both in the laboratory and in the field (Yonge and Nicholls 1931; Reimer 1971; Jokiel and Coles 1974; Kleppel *et al.* 1989). Bleaching can be described as the dissociation of the symbiosis between corals and their endosymbiotic dinoflagellates. It involves the apparent loss of pigmentation due to decreased numbers of their symbiotic dinoflagellates, a reduction of their photosynthetic pigments, or both (Plate 1) (Yonge and Nicholls 1931; Hoegh-Guldberg 1989; Kleppel *et al.* 1989; Porter *et al.* 1989; Jokiel and Coles 1990).

The first reports of coral bleaching occurred in the 1870's (Glynn 1993; Brown 1997), however over the last decade reports of coral bleaching have occurred with increasing frequency and on much larger scales (Gates *et al.* 1992; Brown *et al.* 1994). The majority of

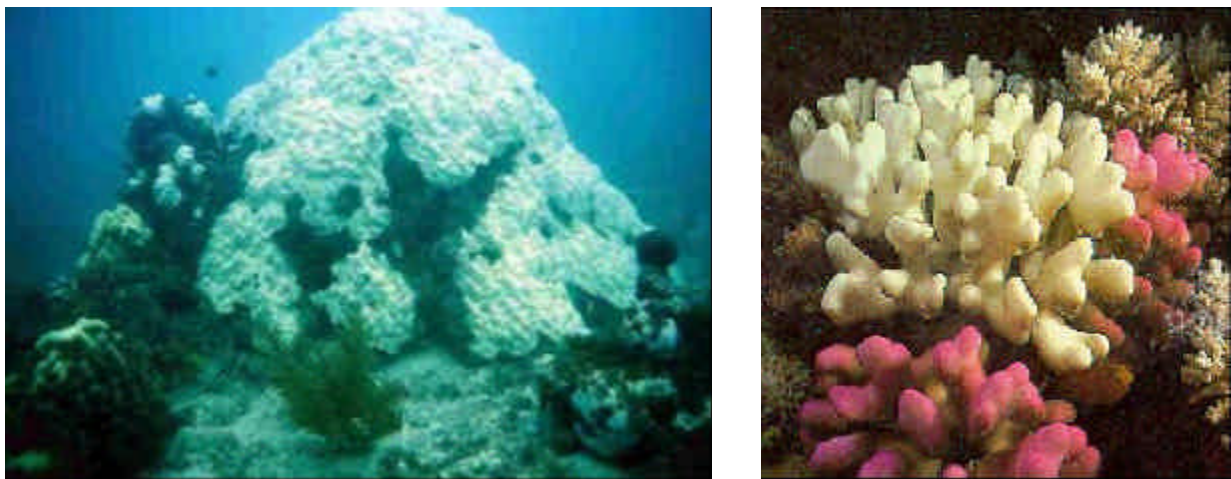


Plate 1: Incidents of coral bleaching in both massive and branching coral species. (www.coral.org/gallery.htm)

reported bleaching events have been correlated with elevated sea surface temperatures, however localised spatial variability both within and between species suggests that more than one environmental factor is involved (Brown 1997; Berkelmans and Willis 1999). Several studies indicate that elevated temperatures act to increase the susceptibility of the endosymbiotic algae of corals to photoinhibition, with the resulting damage leading to expulsion from the coral host (Lesser *et al.* 1990; Roberts 1990; Iglesias-Prieto *et al.* 1992; Hoegh-Guldberg and Jones 1999).

The well established susceptibility of corals to temperature stress has taken on particular significance in the context of global warming, and the occurrence of world wide bleaching events has attracted considerable political, social and scientific comment (Williams and Bunkley-Williams 1990; Buss and Vaisnys 1993; Glynn 1993; Hoegh-Guldberg 1999). Observed temperature responses of corals suggests they are living very close to their upper thermal limits (Jokiel and Coles 1990; Lesser 1997), prompting increasing concern that increasing global temperatures in conjunction with El Niño Southern Oscillation events could have a dramatic influence on reef communities.

Bleaching has also been correlated with decreases in sea surface temperatures (Gates *et al.* 1992), often with more deleterious physiological effects (Coles and Jokiel 1977). It has long been observed that lowered temperatures limit the survival and development of coral reefs, with 18°C accepted as the lower temperature threshold of corals for over a century (Dana 1843; Vaughan 1918). However recent studies have shown that certain species of corals can survive temperatures as low as 11.5°C for several months (Coles and Fadlallah 1991). Nevertheless, a minimum thermal threshold of 16°C still applies for most tropical reef corals. The passage of cold-fronts has been shown to have rapid cooling effects on shallow water carbonate environments, with chilling and mixing of water bodies augmented by associated strong winds (Roberts *et al.* 1982). Upwelling may also affect open ocean reefs, with temperatures dropping several degrees within the changing of tides (Glynn and Stewart 1973). Increased stress associated with warm-water bleaching events in summer may increase the susceptibility of corals to cold-water bleaching. The cumulative effects of summer and winter bleaching events throughout the year could have serious impacts on coral reproduction, growth, and ultimate survival.

This literature review covers the mechanisms involved in coral bleaching in response to both elevated and lowered seawater temperatures. The central role of the coral/algal symbiosis in the formation of coral reef ecosystems and the importance of photosynthesis are discussed. The mechanisms of coral bleaching are described, including the impacts of temperature stress and light as causative agents, with particular focus on the impacts of cold-water bleaching. The mechanisms of zooxanthellae expulsion are presented along with the ecological and social impacts of past and future bleaching events.

2. The Coral/Zooxanthellae Symbiosis

Coral reef communities sustain a large number of mutualistic associations (Glynn 1983) that are thought to have developed as a way of restricting the loss of limiting nutrients in an oligotrophic ecosystem (Muscatine and Porter 1977). Mutualism incurs both benefits and costs for the participant species, and for these mutualistic relationships to have developed the underlying premise is that the benefits for both species must outweigh the costs (Cushman and Beattie 1991).

One of the principle mutualistic symbioses within the coral reef ecosystem is the obligate symbiosis formed by hermatypic corals and their phototrophic dinoflagellates, *Symbiodinium sp* (zooxanthellae) (Muscatine 1990). Scleractinian corals first appeared in the Triassic, and it is widely accepted that their rapid ecological success was directly related to the acquisition of dinoflagellate endosymbionts (Wells 1956; Heckel 1974). The zooxanthellae are located within vacuoles in the cells of the host endoderm (Glider *et al.* 1980; Trench 1987). The zooxanthellae serve as primary producers and supply their coral host with up to 95% of their photosynthetic products, such as sugars, amino acids, carbohydrates and small peptides (Trench 1979; Muscatine 1990). These compounds provide the coral with energy for respiration (Davies 1984), growth, and the deposition of its CaCO_3 skeleton (Muscatine 1990), contributing greatly to the fitness of their host (D'Elia and Wiebe 1990; Muscatine 1990). In return, the zooxanthellae receive essential nutrient compounds of ammonia and phosphate from the waste metabolism of the coral (Trench 1979) (Fig. 1). This tight recycling of nutrients within the association minimises the loss of nutrients (Muscatine and Porter 1977; Falkowski *et al.* 1984), and facilitates the high productivity of corals (Hoegh-Guldberg 1999).

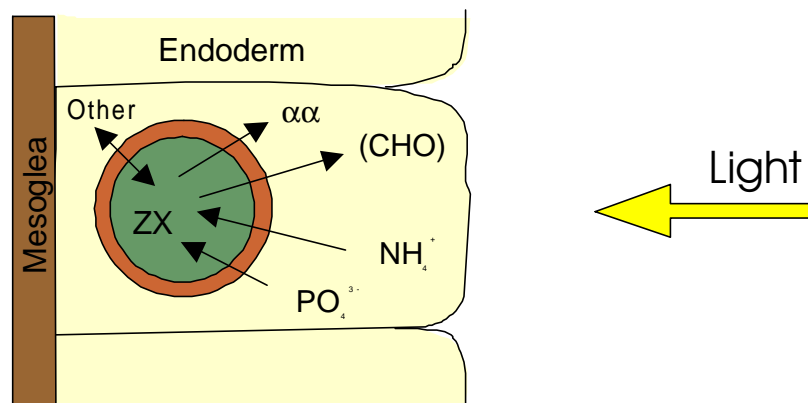


Figure 1: Model of the zooxanthellae/coral symbiosis. ZX = zooxanthellae, (CHO) = carbohydrates, PO_4^{3-} = phosphate, NH_4^+ = ammonium, $\alpha\alpha$ = amino acids.

2.1 *Costs of the coral/algal symbiosis*

The main cost of this association for the corals is that their distribution is limited to places that are favourable for zooxanthellae growth and photosynthesis. Another cost may be the susceptibility of corals to bleaching events. While the dinoflagellate-cnidarian symbioses are typically stable under optimal environmental conditions (Drew 1972; Muscatine *et al.* 1986; Hoegh-Guldberg and Smith 1989), it has been observed that relatively small changes in various physical parameters of the marine environment can disrupt the symbiosis (Glynn 1990). While corals can survive in the absence of their endosymbiotic dinoflagellates in the short term (Franzisket 1969; Johannes *et al.* 1970), the dissociation of the symbiosis results in the loss of a crucial energy source, which can have devastating impacts for the host, including the death of the coral, a reduction in reproductive output (Szmant and Gassman 1990; Ward *et al.* 2000), and decreased rates of growth, and calcification (Glynn 1993).

Certain species of zooxanthellae have been found to be more susceptible to bleaching than others (McField 1999), therefore corals may be disadvantaged simply according to the type of zooxanthellae they contain. Contrary to the initial view that each host coral formed an association with one particular species of dinoflagellate (Trench 1993), it has been determined that a single colony can host dynamic, multi-species communities of *Symbiodinium* sp. (Rowan *et al.* 1997). The composition of these communities can be correlated with levels of irradiance, with some species located preferentially in shaded areas of the colony, and others in the exposed areas (Rowan *et al.* 1997). The type of dinoflagellate present in a particular coral species also changes with depth, and hence different light intensities (Baker *et al.* 1997). It has been proposed that hosting several distinct symbionts is advantageous in that it allows coral communities to adjust to environmental perturbations by selecting for those symbionts that are better suited to changing environmental conditions (Buddemeier and Fautin 1993).

3. **Causes of Bleaching**

There are various factors that can provoke coral bleaching, including reduced salinity (Goreau and Hayes 1994), increased or decreased solar irradiation (Yonge and Nicholls 1931; Hoegh-Guldberg and Smith 1989; Gleason and Wellington 1993), and increased (Hoegh-Guldberg and Smith 1989; Glynn and D'Croz 1990) or decreased water temperature (Jokiel and Coles 1977; Steen and Muscatine 1987). There are also a range of chemical factors, such as herbicides, pesticides, and cyanide (Jones and Hoegh-Guldberg 1999) that evoke the

expulsion of zooxanthellae from their coral host. Consequently, bleaching appears to be a typical physiological response of corals to environmental stress, from either natural or anthropogenic causes (Fang *et al.* 1997).

3.1 *The effects of elevated temperature on bleaching*

Both field and laboratory studies have indicated that elevated temperature is the principal cause of the bleaching events observed at a global scale over the last decade (Hoegh-Guldberg and Smith 1989; Jokiel and Coles 1990; Iglesias-Prieto *et al.* 1992; Iglesias-Prieto 1995; Hoegh-Guldberg 1999), with more than 70% of reported bleaching events associated with unusually high temperatures (28-34°C) (Goreau and Hayes 1994). The advent of the “Hotspot” program, run by the U.S. National Oceanic and Atmospheric Administration, provides further evidence that elevated temperatures are one of the primary factors influencing bleaching events (Goreau and Hayes 1994; Hoegh-Guldberg 1999). The program was developed to accurately predict bleaching events based on the sea surface temperature recorded by satellites days in advance, and succeeded in recording the most severe bleaching event on record in 1998 (NOAA 1998 in Hoegh-Guldberg 1999).

3.2 *Global climate change and ENSO events*

Small scale coral bleaching events have been recorded in response to a variety of environmental disturbances since the 1870's (Glynn 1993; Brown 1997), however over the last decade, acute and chronic bleaching of corals has been reported with increasing frequency (Gates *et al.* 1992; Brown *et al.* 1994). There have been six major episodes of coral bleaching on a global scale since 1979 (Fig. 2) with the most severe event recorded in 1998 (Hoegh-Guldberg 1999), resulting in the destruction of approximately 16% of coral reefs worldwide (Wilkinson 2000). The recent increase in the severity and frequency of bleaching events has attracted significant attention worldwide at political, social and scientific levels (Hoegh-Guldberg 1999). With elevated temperatures indicated as the primary cause of these bleaching events, concern has developed regarding the looming prospect of global climate change, with fears that reef communities may be dramatically influenced by an increase in sea surface temperature (Buss and Vaisnys 1993; Glynn 1993).

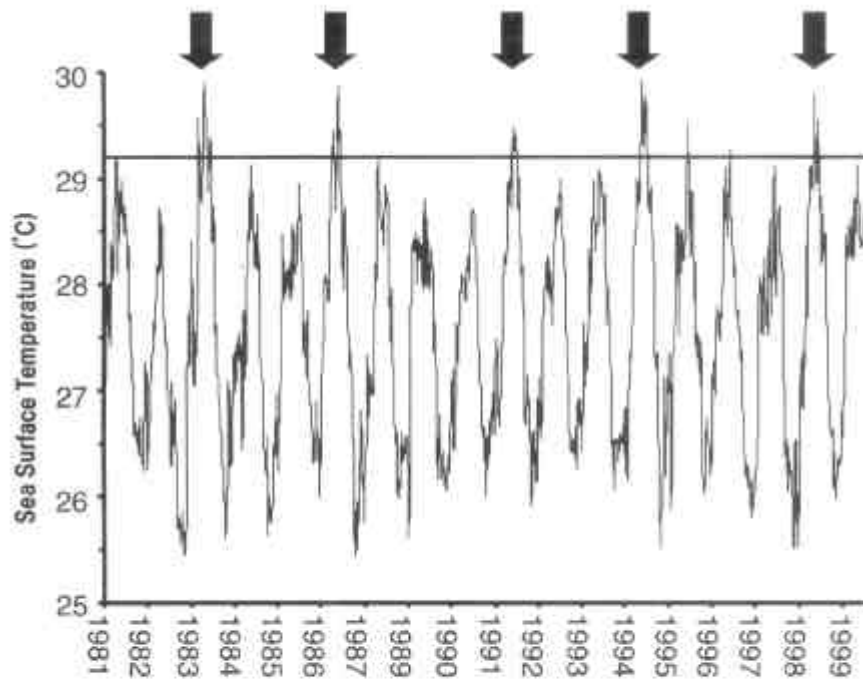


Figure 2: Weekly sea surface temperature data for Tahiti. Arrows indicate bleaching events reported in the literature. Horizontal line indicates the minimum temperature above which bleaching events occur (threshold temperature). (From Hoegh-Guldberg 1999)

Over the last one hundred years, the average temperatures of tropical oceans have increased by 1-2°C (Brown 1997; Cane *et al.* 1997), and this trend is predicted to continue into the next century as a response to increasing emissions of greenhouse gases (Hoegh-Guldberg 1999). Several reports have suggested that corals are already living very close to their upper thermal limits (Jokiel and Coles 1990; Lesser 1997), therefore increasing seawater temperatures as a result of global warming could have devastating impacts for Scleractinian corals (Glynn 1993; Brown 1997).

Based on trends in sea-surface temperatures from the last twenty years, a Global Climate Model was developed to simulate future sea temperatures (Hoegh-Guldberg 1999). When compared with the thermal thresholds of various species using data derived from current bleaching events (Glynn 1993; Brown 1997; Jones *et al.* 1998; Hoegh-Guldberg 1999), the frequency and intensity of future coral bleaching events could be estimated. This model predicts that global warming coupled with ENSO events will generate increasing seawater temperatures over the next 100 years, indicating that unless corals are able to adapt to these increased temperatures, bleaching events will occur on a yearly basis (Hoegh-Guldberg 1999).

Until the present, most of the recorded bleaching events have been correlated with the occurrence of El Niño Southern Oscillation (ENSO) (McCulloch *et al.* 1998; Hoegh-Guldberg 1999). ENSO is a large-scale dynamic interaction across the Pacific and Indian Oceans involving the major low-latitude atmospheric pressure centres (Reviewed in Glynn 1990). One of the main impacts of ENSO is to increase sea surface temperatures in the eastern Pacific, and in equatorial regions. This substantial increase in temperature caused by ENSO acts to raise sea-surface temperatures above the upper thermal threshold of corals, resulting in a bleaching event (Hoegh-Guldberg 1999). However an aspect of global climate change that is often neglected is the secondary impact of La Niña, which often results in cooler average winter temperatures that often drop below the lower thermal threshold of corals (Fig. 3). Bleaching events caused by sequential El Niño and La Niña years may have devastating impacts on coral growth and reproduction.

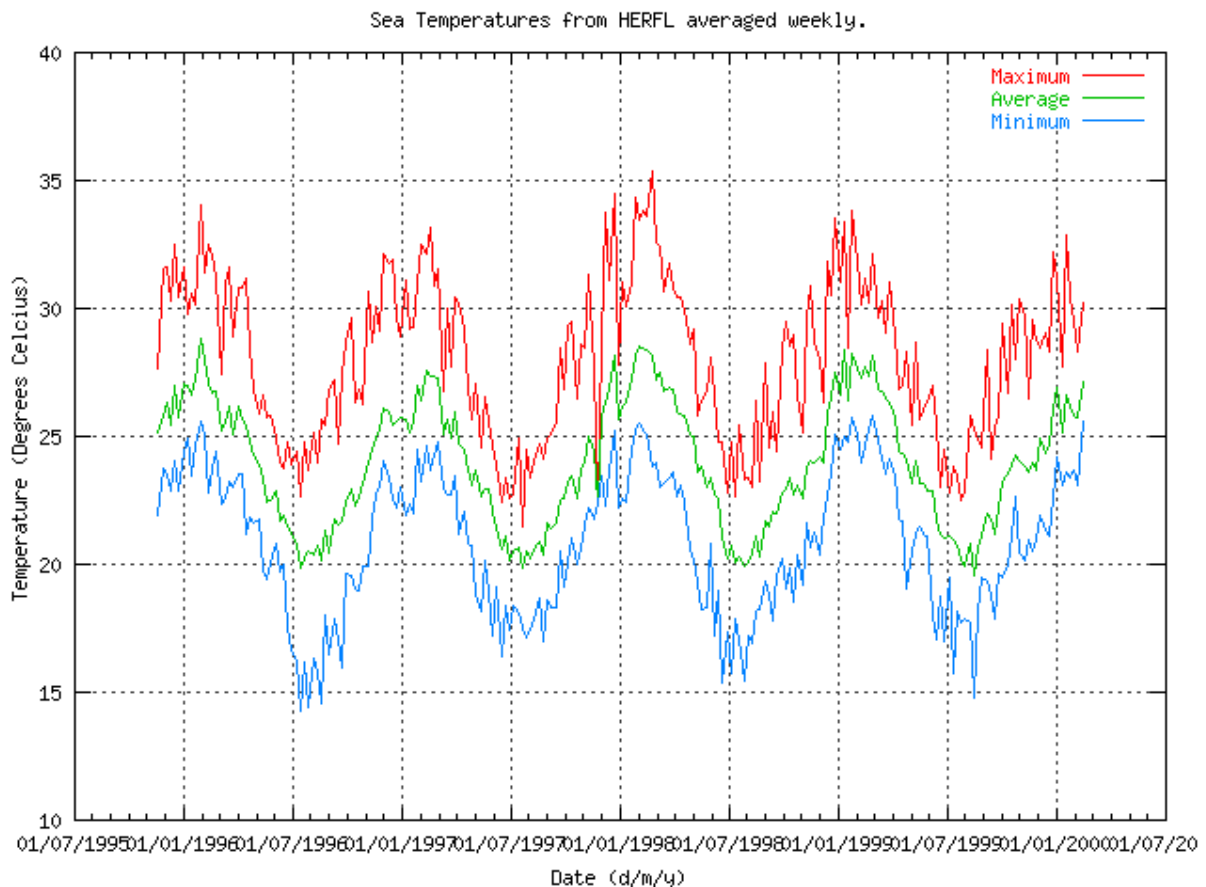


Figure 3: Average sea surface temperatures on Heron Island Reef Flat. The horizontal line at 15°C indicates the lower thermal threshold of most coral species. (Courtesy of GBRMPA)

4. Cold Water Bleaching in Corals

Lowered temperatures have been recognised to exert a strong influence on the development and distribution of coral reefs for over a century (Dana 1843; Vaughan 1918). This is evident by the absence of reef development on the western sides of continents, which are typically influenced by cooler polar currents. While some reef corals can survive in areas with lower average seawater temperatures, they typically fail to form reefs (Glynn and Stewart 1973; Coles and Fadlallah 1991). This can probably be explained by decreased growth rates of corals at cooler temperatures (Jokiel and Coles 1977), or the inability of corals to compete with macroalgal growth as a result of temperature-induced stresses (Walker *et al.* 1982). Lower temperatures also limit the structure and composition of coral reefs in both tropical and subtropical environments (Glynn and Stewart 1973; Jokiel and Coles 1977; Roberts *et al.* 1982). The passage of cold-fronts has been shown to have rapid cooling effects on shallow carbonate environments, with chilling and mixing of water bodies augmented by associated strong winds (Roberts *et al.* 1982). Upwelling may also affect open ocean reefs, with temperatures dropping several degrees within the changing of tides (Glynn and Stewart 1973). The sudden drops in temperature induced by either atmospheric chilling or intense upwelling have been observed to induce severe coral bleaching and coral death (Glynn and Stewart 1973; Hudson 1981; Coles and Fadlallah 1991; Glynn 1993).

4.1 *Physiological effects of cold-water stress*

The physiological consequence of sustained low temperatures for the stability of coral-algae symbioses is well documented (Glynn and Stewart 1973; Coles and Fadlallah 1991). In a series of lab experiments, Mayor (1916), (Mayer 1916) identified 16°C as the critical thermal threshold at which corals lose their ability to capture food, and that prolonged exposure to temperatures between 13-15°C is sufficient to kill most tropical coral species (Mayer 1914). This is supported by experiments on Hawaiian reef corals that demonstrated that corals could survive only 1-2 weeks of continuous exposure to 18°C or less (Jokiel and Coles 1977). The effects of cold-water stress have also been observed on numerous occasions in the field. A drop in seawater temperatures below the 16°C threshold of corals was recorded over an 8 day period at the Bahama Banks, in Florida Bay, resulting in widespread coral bleaching and subsequent mortality (Hudson 1981; Roberts *et al.* 1982; Walker 1992). Similar widespread mortality of *Acropora* thickets was observed following cooling of Persian Gulf waters (Shinn 1976). In addition to bleaching responses, temperature has also been correlated with a general decline in coral growth (Glynn and Stewart 1973). However, the effects of reduced

temperatures on coral survival and growth appears to be species specific, and geographically variable, with recent studies in the Western Arabian Gulf showing that certain species of corals can survive temperatures as low as 11.5°C for several months (Coles and Fadlallah 1991). Therefore cold-water bleaching events are analogous to warm-water bleaching events in that bleaching occurs once the thermal limit of a particular coral is exceeded.

5. Spatial variability in bleaching events

Coral bleaching affects a diverse array of corals, with bleaching recorded in 101 species of Scleractinia in 1998 on the inshore reefs of the Great Barrier Reef (Baird and Marshall 1998). However, various studies have indicated that there is considerable variation in the thermal tolerance of different species (Edmondson 1928; Coles and Jokiel 1978; Marshall and Baird 2000). It has been hypothesised that these differences are caused by differences in the susceptibilities of coral species to thermal stress, and the different genotypes of their endosymbiotic zooxanthellae. A study by McField (1999) concluded that if corals contained a certain type of zooxanthellae, they were more susceptible to bleach than others. It has also been proposed that there are differences in the susceptibility of different types of corals, with “weedy” species, such as *Pocillopora* or *Acropora* being more susceptible to bleaching (Hoegh-Guldberg *et al.* 1997). Interspecific differences in susceptibility to disturbance are a critical aspect of community dynamics as they can lead to changes in community structure and species diversity (Connell 1978; Hughes 1994; McField 1999).

Differences in bleaching severity have also been observed between geographically separate populations of the same species (Coles *et al.* 1976; Marcus and Thorhaug 1981; Berkelmans and Willis 1999). This could be explained by a variety of factors, such as differences in the severity of the temperature increase between different locations, or genetic variation between coral and/or zooxanthellae from the different locations (Buddemeier and Fautin 1993; Rowan and Knowlton 1995). The thermal history of a reef can also have a substantial effect on the reaction of individuals, populations and communities to increased temperatures (Jokiel and Coles 1990; Berkelmans and Willis 1999). For example, reefs that have been exposed to relatively higher temperatures in the past are less likely to bleach than similar reefs from cooler environments (Marshall and Baird 2000).

Localised differences in bleaching events have also been observed, with gradations in bleaching intensity observed within colonies (Brown *et al.* 1995). The tendency of corals to

bleach can also be substantially different between two adjacent colonies (Atwood *et al.* 1992). Typically, corals are observed to bleach with the greatest intensity on the upper sides of the colony (Jokiel and Coles 1977; Jones 1997). In a more recent study in the Caribbean, Rowan *et al.* (1997) observed a curious pattern of bleaching with shallower colonies bleached preferentially in shaded places and deeper colonies bleached preferentially in unshaded places. Variation has been observed at even smaller scales, with some corals losing more zooxanthellae from the more exposed oral tissues than deeper tissues (Brown *et al.* 1995). These patterns in bleaching cannot be explained by variations in seawater temperatures alone, and there is evidence to suggest that light intensity plays a key role in the susceptibility of corals to thermal stress (Gleason and Wellington 1993; Brown *et al.* 1994; Jones *et al.* 1998; Hoegh-Guldberg 1999).

6. Photoinhibition: the synergistic effects of high light and elevated temperatures

6.1 What is Photoinhibition?

Photoinhibition has been described as the light-dependent inhibition of photosynthesis (Fig. 4) (Powles 1984; Greer and Laing 1991). Functionally, it can be described as the decreased capacity of a photosystem to capture and process photons (Long *et al.* 1994; Osmond 1994), and is characterised by the accumulation of photochemically inactive PSII reaction centres (Krause 1994). This typically results in a decrease in the overall photosynthetic rate (Richter *et al.* 1990). Photoinhibition is one of the daily challenges faced by most photosynthetic organisms (Walker 1992; Long *et al.* 1994; Hoegh-Guldberg and Jones 1999), for while light is beneficial, in excess it can potentially cause irreversible damage to the photosynthetic machinery (Walker 1992; Foyer *et al.* 1994; Long *et al.* 1994; Osmond 1994). Photoinhibition occurs where the utilisation of energy by the fixation of CO₂ is exceeded by the amount of incoming light energy (Greer and Laing 1991). This results from a reduction in photosynthetic electron transport combined with continued high absorption of excitation energy, which then leads to inactivation of or damage to PSII from the production of toxic oxygen species (Osmond 1994; Lesser 1996). It has been proposed that the reduction of PSII efficiency may act as a protective mechanism to prevent damage to the photosynthetic apparatus, rather than indicating the degradation of the D1 protein of PSII. Therefore it is important to discriminate between the inactivation of PSII as a reversible downregulation of photosynthesis, and the irreversible effects of photodamage (Critchley and Russell 1994).

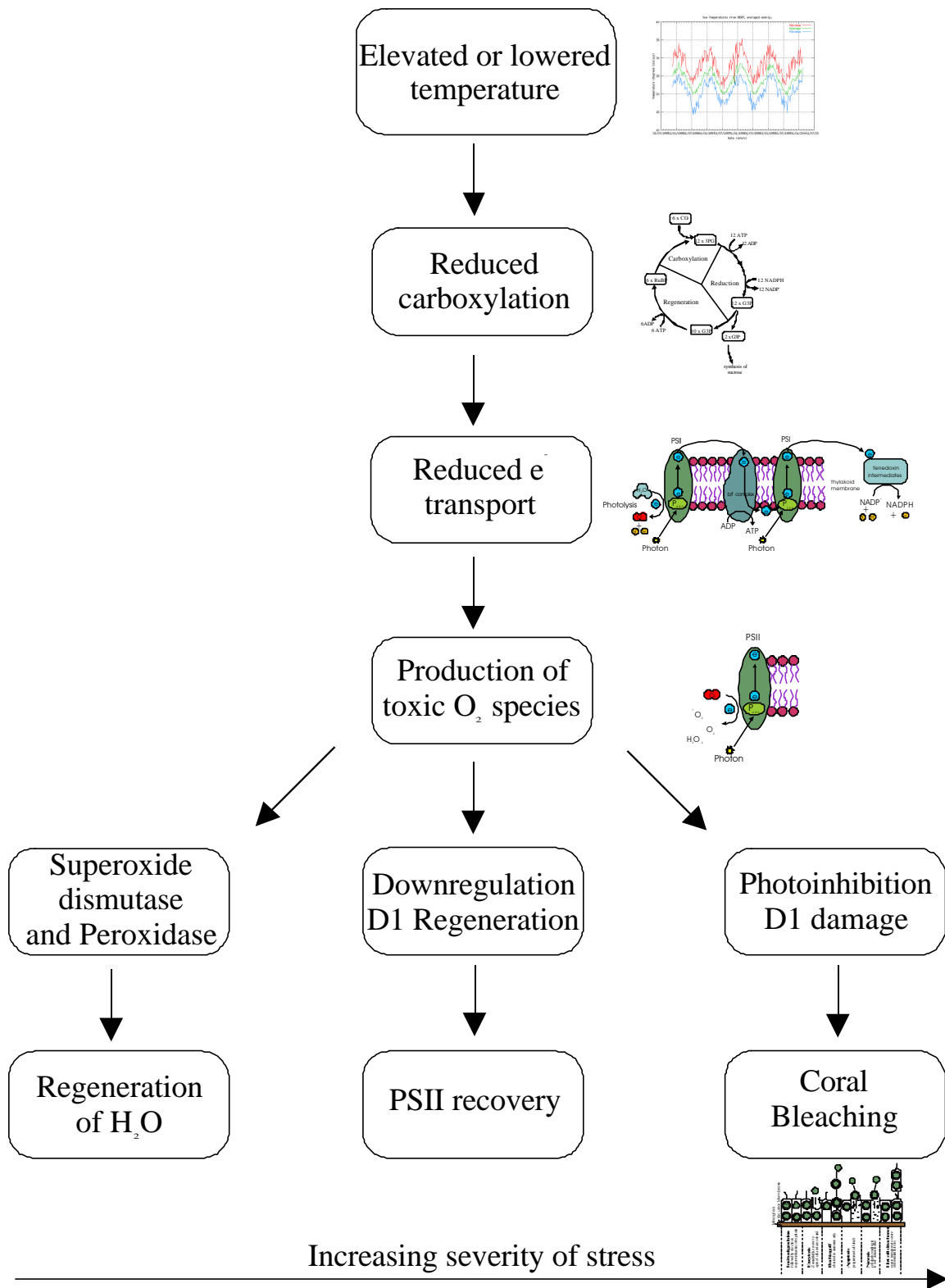


Figure 4: Flow chart of the mechanisms involved in photoinhibition.

6.2 *Mechanisms of Oxygen Toxicity:*

Active oxygen species are produced by a variety of metabolic processes, however the major source of active oxygen species in plant tissues is the photosynthetic electron transport system (Asada 1994). In photosynthesis, molecular oxygen is produced from the oxidation of water by the photosynthetic electron transport chain (Foyer *et al.* 1994). Oxygen can also be used as an electron acceptor, a reaction that results in the formation of singlet oxygen ($^1\text{O}_2$) and superoxide radicals (O_2^-) (Fridovich 1986; Foyer *et al.* 1994). Singlet oxygen is highly destructive as it reacts with most biological molecules (Knox and Dodge 1985). Superoxide is also highly toxic with several cellular targets, however its primary impact is an indirect one, as it gives rise to more powerful oxidants such as hydrogen peroxide (H_2O_2) and the hydroxyl ion (HO) (Fridovich 1986). The principal sites of damage from these toxic oxygen species include the primary carboxylating enzyme, Rubisco, and Photosystem II, in particular, the D1 protein of PSII, which appears to have very little protection against oxidative damage (Asada and Takahashi 1987; Richter *et al.* 1990; Tschiersch and Ohmann 1993). Damage to the D1 protein caused by reactive oxygen is irreversible, and can be corrected only by the enhanced synthesis and replacement of the protein (Long *et al.* 1994). Under normal light conditions, PSII undergoes a complex cycle of damage, degradation and repair, caused by damage to the D1 protein by active oxygen species. When the rate of damage exceeds the rate of repair, photoinhibition results (Powles 1984). However, more recent studies have suggested that oxidative damage to PSII is a secondary step following damage to the Calvin cycle (Jones *et al.* 1998). Either pathway indicates that toxic oxygen species have a key role in the mechanism of PSII damage, and thus photoinhibition (Richter *et al.* 1990).

To counteract the toxic effects of these active oxygen species, plants have developed a highly efficient antioxidative defence system (Foyer *et al.* 1994). The enzymes superoxide dismutase, catalase, and ascorbate peroxidase inactivate superoxide radicals and hydrogen peroxide, thereby preventing formation of hydroxyl radicals, and subsequent cellular damage (Fridovich 1986). However, with increased temperatures the capacity to make or accumulate superoxide dismutase is decreased, resulting in increased amounts of active oxygen species. Similarly, slightly elevated levels of oxygen have the capacity to overpower a cell's defence systems (Dyken and Shick 1982). This could be of particular importance for symbiotic

marine animals that harbour phototrophic endosymbionts that generate excess oxygen, thereby creating hyperbaric oxygen levels in the tissues of the host (Dykens and Shick 1982).

6.3 *Significance of D1 protein*

Photosystem II is a key component of the photosynthetic machinery of plants, as it produces the oxygen necessary to extract energy stored in organic molecules (Barber 1995). However, the molecular processes involved in the production of oxygen also produce toxic oxygen species, which attack PSII at the D1 protein (Richter *et al.* 1990; Tschiersch and Ohmann 1993). This means that PSII is continuously going through a cycle of damage and repair. At low and moderate light intensities the rate of damage to the PSII reaction centre is usually balanced by the repair process, which involves synthesis of D1 protein (Barber 1995). When the rate of damage exceeds the rate of repair, photoinhibition results (Powles 1984).

It has been suggested that the D1 protein of PSII has developed to provide protection against photoinhibition in plants that are exposed to high light or other environmental stresses (Richter *et al.* 1990; Foyer *et al.* 1994). While the degradation of D1 protein caused by oxidative stress may appear destructive, it may act like a fuse by stopping further production of active oxygen species, and thus preventing widespread damage to the rest of PSII (Richter *et al.* 1990).

6.4 *Factors exacerbating photoinhibition*

It has been shown that the incidence of photoinhibition is greatly increased by exposure to environmental stresses (Elstner *et al.* 1988) such as cyanide (Jones and Hoegh-Guldberg 1999), low or high temperatures (Greer and Laing 1991; Foyer *et al.* 1994) or greatly increased levels of visible or ultra-violet radiation (Lesser 1996). These additional stress factors increase the susceptibility of plants to photoinhibition as they cause perturbations in metabolism, which often leads to large decreases in the capacity for photosynthetic carbon assimilation (Wise and Naylor 1987; Foyer *et al.* 1994). Photoinhibition is also exacerbated by anthropogenic impacts, such as atmospheric pollutants (Shimazaki and Sugahara 1980), herbicides and heavy metals (Foyer *et al.* 1994). There are a variety of mechanisms by which these man-made compounds can affect photoinhibition, including: 1) the direct involvement in free radical formation, 2) inhibition of biosynthetic pathways with production of a photoreactive intermediates, 3) direct photodynamic action in plants (Foyer *et al.* 1994).

Exposure to additional environmental stresses reduces the ability of a plant to assimilate energy, causing lower levels of incident irradiance to become inhibitory (Foyer *et al.* 1994). In addition, certain protective responses against oxygen toxicity such as the production of superoxide dismutase may lose effectiveness (Dykens and Shick 1982). Chilling temperatures have been found to strongly exacerbate photoinhibition in both chilling-sensitive and chilling-tolerant plants (Smillie *et al.* 1988; Greer 1990). Consistent with higher temperatures, the extent of photoinhibition is determined by the inactivation of PSII reaction centres (Somersalo and Krause 1990; Krause 1994).

7. Photoinhibition in Corals

As in higher plants, photoinhibition is a natural characteristic of the photosynthetic process of the endosymbiotic dinoflagellates of corals (Hoegh-Guldberg and Jones 1999). In the shallow reef environment many species are exposed to extremely high levels of solar irradiance on a daily basis (Shick *et al.* 1996). While corals have developed mechanisms to cope with these high light levels, when in conjunction with other environmental variables, increased rates of photoinhibition have been shown to occur (Lesser and Shick 1989; Iglesias-Prieto *et al.* 1992; Lesser 1996). Factors linked to reductions in photosynthetic rates in zooxanthellae include exposure to elevated temperatures (Iglesias-Prieto *et al.* 1992; Fitt and Warner 1995), increased UV (Jokiel and York Jr 1984; Lesser and Shick 1989), hyperoxia and lowered temperatures (Steen and Muscatine 1987). As all of these factors result in the subsequent expulsion of zooxanthellae from the host tissues, photoinhibition has been implicated as a causative agent of coral bleaching.

The mechanisms of photoinhibition in corals appear to be similar to those in higher plants, with high light and physiological hyperoxia acting synergistically to produce active oxygen species (Lesser *et al.* 1990). As in other systems, the effect of oxygen radicals includes damage to photosystem II at the D1 protein (Richter *et al.* 1990; Tschiersch and Ohmann 1993), as well as several other cellular targets. It has been proposed that the resulting cellular damage caused by oxidative stress results in an energetic cost to the coral host, either in terms of decreased translocation of photosynthate, or exposure to highly reactive oxygen radicals (Lesser and Shick 1989). As a result, the zooxanthellae are expelled from the host tissues, probably as a protective mechanism against further oxidative stress (Lesser 1997).

Photoinhibition of zooxanthellae may have an even greater impact at increased or decreased temperatures as the permeability of membranes is affected, meaning that coral tissues may be directly attacked by toxic oxygen species. This is supported by evidence that high temperatures induce the synthesis of catalase in coral cells, a protective enzyme against toxic oxygen species (Lesser *et al.* 1990). Another study by Lesser (1997) found that the addition of exogenous antioxidants to corals undergoing temperature stress increased photosynthetic rates and prevented the expulsion of zooxanthellae. This observation confirms a role for oxidative stress in the bleaching process.

Photoinhibition also provides a way to explain intra-specific spatial variability in patterns of bleaching. Coral colonies can act as hosts to several different species of endosymbiotic dinoflagellates, with the composition of these communities following gradients of solar irradiance (Rowan *et al.* 1997). The amount of light received by each zooxanthella is dependent upon its location within in the colony with regard to orientation and shading. Host tissues also modify the amount of light received by zooxanthellae, and depending on the density of zooxanthellae, sometimes self-shading can occur (Trench and Fisher 1983; Iglesias-Prieto and Trench 1994). Previous studies have indicated that *Symbiodinium microadriaticum* has both sun-loving and shade-loving genetic variants, and that the distribution of these is dependent upon the host species (Jokiel and York Jr 1984). Observed patterns of bleaching where shaded portions of colonies tend to bleach first could be explained by different susceptibilities of different genetic strains of zooxanthellae to photoinhibition (Buddemeier and Fautin 1993; Rowan and Knowlton 1995). An alternative possibility is the susceptibility of zooxanthellae to photoinhibition dependent upon their respective light history, as cells that live under continuous low irradiance are much more susceptible to photoinhibition, and its subsequent effects (Richter *et al.* 1990). This susceptibility is possibly related to the light-dependent repair of PSII, as plants that are grown in shaded or low-light environments appear to have a lowered capacity for repair than plants grown in full sunlight (Foyer *et al.* 1994).

7.1 *Mechanisms of bleaching in response to cold-water stress*

The mechanisms of coral bleaching at lowered temperatures appear similar to those observed in response to elevated temperature stress. It is well documented that chilling temperatures intensify photoinhibition in higher plants (Lyons 1973; Smillie *et al.* 1988; Aro *et al.* 1990; Greer 1990; Greer and Laing 1991; Foyer *et al.* 1994; Long *et al.* 1994). Zooxanthellae

exposed to cold-water conditions show decreased photosynthetic rates, increased respiration and a reduction in the numbers of viable cells (Steen and Muscatine 1987). These responses implicate photoinhibition as a causative agent of coral bleaching following exposure of corals to cold-water stress. This is supported by evidence that bleaching tends to occur on the exposed upper surfaces of the corals, while the tissues in shaded regions of the colony survived (Jokiel and Coles 1977). The effects of photoinhibition in response to lowered temperatures appear to have a more deleterious effect than elevated temperatures. Coral recovery is often greatly reduced (Jokiel and Coles 1977), with mortality of corals observed months after cold-water stress events are recorded (Hudson 1981; Roberts *et al.* 1982). This could be related to the damaging effects of lowered temperatures on the metabolism of animal cells (Watson and Morris 1987), which can increase membrane permeability, resulting in metabolic disorder. In addition to photo-oxidative stress induced by the photoinhibition of photosynthesis, lowered temperatures appear to have a more deleterious physiological effect. As a result, the principle mechanism of release of zooxanthellae involves the sloughing off of intact endodermal cells containing zooxanthellae in various stages of degradation (Muscatine *et al.* 1991).

8. Mechanisms of zooxanthellae expulsion

Recent findings suggest that there are several different mechanisms by which endosymbiotic dinoflagellates can be expelled from their cnidarian host tissue when corals are exposed to environmental perturbations (Gates *et al.* 1992; Brown *et al.* 1995). It appears that no single mechanism operates exclusively during a bleaching event, and that the mechanisms are not necessarily species specific (Brown *et al.* 1995). However, there may be a correlation between the type of the stress imposed upon the coral, as well as its severity and duration, and the mechanism of coral/algal dissociation. The mechanisms involved may also differ depending on whether the environmental stress principally affects the host cells (Gates *et al.* 1992) or the algal symbionts (Glynn and D'Croz 1990; Lesser *et al.* 1990; Iglesias-Prieto *et al.* 1992).

The exact mechanism responsible for the release of zooxanthellae in corals in response to cold water shock is not known (Stimson and Kinzie 1991), however, there are observations of the effect of cold-water stress on the anemones *Aiptasia pulchella* and *A. pallida*. The primary mechanism by which zooxanthellae are released involves the exocytosis of algal cells from the epithelium into the coelenteron (Steen and Muscatine 1987). It can be assumed

that bleaching of corals caused by cold water stress would be induced by a variety of different mechanisms of zooxanthellae release, as in other bleaching events.

At present, there are five proposed cellular mechanisms by which zooxanthellae could be released from the host coral, as determined from histological analyses in both field and laboratory based studies (Fig. 5) (Gates *et al.* 1992; Brown *et al.* 1995; Le Tissier and Brown 1996; Brown 1997):

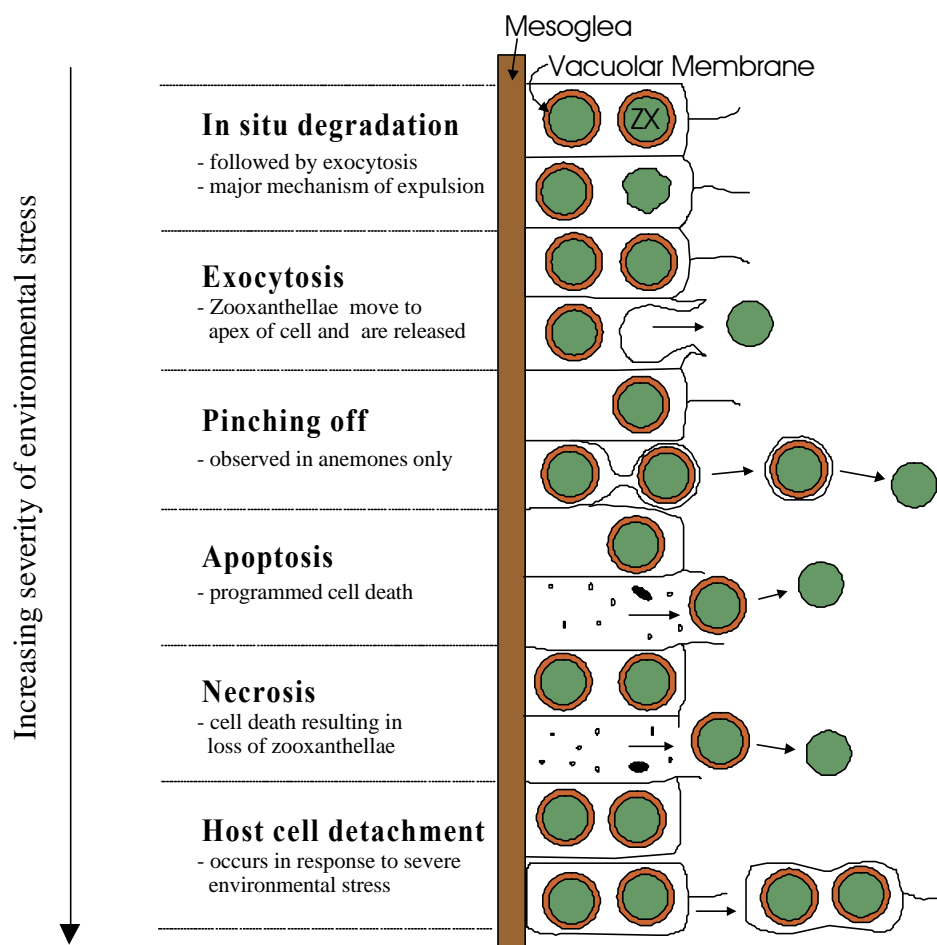


Figure 5: The possible mechanisms of zooxanthellae expulsion with increasing severity of environmental stresses. ZX = zooxanthellae (Adapted from Gates, Baghdasarian *et al.* 1992)

1) *In situ zooxanthellae degradation*

This appears to be the major mechanism for the reduction of zooxanthellae numbers, following a bleaching event in Thailand in 1991 (Brown *et al.* 1995). Histological analyses revealed the degradation of zooxanthellae in situ, which was typically followed by the exocytosis of the damaged cell from the endoderm into the

coelenteron (Brown 1997). Similar observations were recorded following solar bleaching in intertidal corals (Brown *et al.* 1994; Le Tissier and Brown 1996), and bleaching related to elevated seawater temperatures in Panama during the 1982-1983 El Nino event (Glynn *et al.* 1985).

2) *Exocytosis*

This mechanism was first observed by Yonge and Nicholls (1931) following the exposure of various corals to different light regimes. They reported that zooxanthellae accumulated in the absorptive region of the mesenterial filaments, and were thence expelled via the coelenteron in clumps of mucus. A similar mechanism of zooxanthellae release was observed by Coles (1973) following the exposure of Hawaiian reef corals to temperature stress. More recently, exocytosis of zooxanthellae was suggested as the preferred mechanism of release in the anemone *Aiptasia pulchella* after exposure to chilling temperatures for 8 hours (Steen and Muscatine 1987). It was hypothesised that the algae move towards the apex of the host cells, whereby they are released into the coelenteron by exocytosis. They are then discharged from the coelenteron as individual cells, or as pellets of cells in various stages of disintegration (Steen and Muscatine 1987).

3) *Pinching off*

This mechanism has been observed in the anemone *Aiptasia pallida*, which has a symbiotic association with the dinoflagellate, *Symbiodinium microadriaticum* (Glider 1983). The mechanism involves the pinching off of the distal portion of the host cell, which results in the release of the endosymbiotic dinoflagellate, surrounded by the pinched off plasma membrane of the host (Glider 1983). At present, there are no known observations of this mechanism of zooxanthellae release in corals.

4) *Apoptosis and Necrosis*

Programmed cell death, or apoptosis, is a crucial component of animal development. It involves the activation of a cascade of “suicide” proteins, which dismantle cellular proteins and DNA, leading to cell death (Campbell 1996). In many cases, cells are programmed to die to prevent other cells from being damaged by harmful enzymes or metabolites. In the case of coral bleaching, the death of endodermal cells containing zooxanthellae may prevent other cells from being damaged by the toxic oxygen

species produced during photoinhibition. Necrosis also results in cell death, however it only occurs in response to localised injury. Both mechanisms result in the release of the zooxanthellae associated with remnants of the host cell (Searle *et al.* 1982).

5) *Host cell detachment*

This mechanism has previously been described as the primary mechanism by which zooxanthellae were released from both corals and anemones exposed to high temperatures (Gates *et al.* 1992) and involves the detachment of intact endodermal cells from the host tissue, with their complement of intracellular zooxanthellae. However it has been argued that this response only occurs following exposure to extreme environmental stress (Brown *et al.* 1995). In the above laboratory experiment by Gates *et al.* (1992), the corals were exposed to temperatures 10°C above ambient temperatures, a scenario that is unlikely to occur naturally. Such a dramatic change in temperature is likely to have had a profound impact on the metabolism of the host, which could explain the subsequent loss of damaged host cells. In comparison, field studies following natural bleaching events show that there is little apparent ultrastructural damage to host endoderm cells in the majority of bleached corals (Brown *et al.* 1995; Le Tissier and Brown 1996). This supports the hypothesis that host-cell detachment is an extreme response to environmental stress (Buddemeier and Fautin, 1993), which is commonly followed by tissue death and mortality of the host coral (Brown *et al.* 1995).

9. **Impacts of coral bleaching**

9.1 *Physiological effects*

The immediate effects of bleaching on coral hosts have been well documented over the last decade. One of the initial responses appears to be a decrease in photosynthetic rates caused by photoinhibition following exposure to sublethal temperature perturbations (Iglesias-Prieto *et al.* 1992; Fitt and Warner 1995) and/or UV radiation (Jokiel and York Jr 1984; Lesser and Shick 1989; Lesser 1996). This is typically followed by the expulsion of zooxanthellae from the host endoderm, a decrease in photosynthetic pigments or both (Yonge and Nicholls 1931; Hoegh-Guldberg 1989; Kleppel *et al.* 1989; Porter *et al.* 1989; Jokiel and Coles 1990). Zooxanthellae typically provide their coral host with organic compounds produced through photosynthesis (Muscatine 1990), which is believed to provide energy for the maintenance, growth and reproduction of many reef corals (Szmant and Gassman 1990). Therefore, the

loss of zooxanthellae, and the observed decrease in photosynthetic capacity can be translated into a significant decrease in cellular growth rates (Lesser, 1996), calcification (Muscatine 1990) and reduced reproductive capacity of corals (Porter *et al.* 1989; Szmant and Gassman 1990; Gleason and Wellington 1993; Ward *et al.* 2000). Other effects include increased respiration rates, and declines in coral protein, lipid and carbohydrate content (Kleppel *et al.* 1989; Glynn 1990; Jokiel and Coles 1990), which can be expected as corals utilise reserve products to support basic metabolism (Szmant and Gassman 1990). Bleached corals also appear more susceptible to invasion by parasites, bacteria (Kushmaro *et al.* 1996) and other diseases, which can ultimately result in coral death (Kleppel *et al.* 1989).

9.2 Ecological effects

Decreased growth rates, and reduced reproductive success could have a profound impact on the structure of coral communities, potentially resulting in decreased coral cover, reduced species diversity, and changes in community composition (Connell 1978; Connell 1997). Increased sea temperatures mean that aragonite saturation of water is reduced, depressing the calcification rates of corals (Done 1999). This may increase the susceptibility of corals to storm damage, and invasion by boring organisms (Mokady *et al.* 1998). The resulting loss of limestone infrastructure could thereby affect the carrying capacity of the ecosystem for other reef organisms (Done 1999). Reduced growth and calcification rates also act to decrease the capacity of corals to compete for space with other, faster growing species, such as macroalgae, coralline algae, sponges, or other invertebrates (Glynn 1993). Macroalgae already dominate many coral reefs in the Caribbean, and the additional reduction in the competitiveness of corals could threaten the long-term integrity of coral structures (McField 1999). Similar changes in community composition have been observed on the inner shelf of the Great Barrier Reef, with changes from a hard coral dominated state to a macroalgal or soft coral dominated state (Wachenfeld *et al.* 1998). Changes in community structure of coral reefs could also have important impacts for the majority of other organisms that live within these ecosystems (Glynn 1993).

Anthropogenic impacts on coral reefs have increased dramatically in recent times due to increasing development within coastal areas and altered land use patterns (Reviewed in Birkeland 1997). Increases in detrimental activities, such as clear-cut logging, land clearing, coastal development, agricultural and landscape fertilisation, fishing, sewage disposal, pesticide use, and accidental chemical spills have all caused unequivocal damage to coral

reefs on local scales (Glynn 1993). While these impacts appear relatively minor in contrast to major bleaching events, it has been suggested that exposure to these anthropogenic impacts could act to increase the susceptibility of corals to thermal stress, and thereby increase the occurrence of bleaching events.

9.3 *Socio-economic effects*

Coral reefs have an important role in the primary production of the ecological systems of tropical oceans. They provide the basis for a complex food web and harbour thousands of species, many of which provide a sustainable harvest (Spurgeon 1002). Fisheries in coral reef areas generate significant wealth and create employment for millions of fishers worldwide, as well as providing a significant source of protein for many third world countries (Carte 1996; Bryant *et al.* 1998). Coastal fisheries also benefit from the presence of coral reefs, which allow the formation of protected habitats such as mangroves and seagrasses, both of which provide nursery habitat for up to 90% of commercial fish species (Hoegh-Guldberg *et al.* 2000).

Reefs also represent a crucial source of income and resources through their role in tourism, generating billions of dollars annually (Jameson *et al.* 1995). In the case of small island nations, tourism is the driving force behind the economy, with thousands of people depending on the 'tourist dollar' for livelihood (Hoegh-Guldberg *et al.* 2000). Therefore, the degradation of coral reefs will have profound effects worldwide, with the expected costs of these impacts exceeding billions of dollars annually, and extensive economic and social impacts for millions of people (Dustan 1998).

9.4 *Potential for acclimation and adaptation:*

Observed temperature responses of corals suggests that in many cases they are living very close to their upper thermal limits (Jokiel and Coles 1990; Lesser 1997), which can be viewed implicitly as evidence that corals have been unable to adapt to increases in temperature over the last few centuries (Hoegh-Guldberg 1999). However, the differences in susceptibility between coral species to both increased temperatures and higher irradiance indicates a potential for acclimation and adaptation (Iglesias-Prieto and Trench 1994; Fitt and Warner 1995; Warner *et al.* 1996; Brown 1997)

The potential for thermal acclimation in corals was first suggested following a series of experiments whereby colonies of *Montipora verrucosa* displayed increased survivorship at high temperatures following incubation at 28°C, compared with colonies incubated at lower temperatures (Coles and Jokiel 1978). This is confirmed by general observations that individual coral colonies exposed to high temperature environments can survive at temperatures a few degrees higher than other colonies of the same species that are exposed to lower temperatures (Jokiel and Coles 1990). This highlights the importance of thermal history of corals with regard to their susceptibility to bleaching events (Marshall and Baird 2000). Coral reefs in the Western Arabian Gulf are routinely exposed to an annual seawater temperature range of 24.8°C, which exceeds the temperature extremes reported for any other reef in the world by nearly 5°C (Coles 1988; Coles and Fadlallah 1991). For corals to survive these extreme temperatures, it can be supposed that some form of acclimation or adaptation has occurred. However, it is likely that these adaptations probably took place over a long time period, and whether corals have the ability to adapt over shorter time scales remains to be proven.

Only one study implicates short-term thermal acclimatisation in the recovery of corals located downstream from a thermal effluent stream of a power plant, following a natural bleaching event (Meesters and Bak 1993). However, another study by Berkelmans and Willis (1999) showed significant differences in the upper thermal limits of 3 different coral species on a seasonal basis. This implies that at least some corals may be capable of short-term thermal acclimatisation (Berkelmans and Willis 1999). It must also be remembered that numerous coral species have survived several warm epochs since the Pliocene, some with possibly warmer climates than today (Crowley and North 1991). The mechanism by which this occurred is unknown, but could implicate the adaptation of corals to warmer sea temperatures. Alternatively, corals may have retreated to cooler waters closer to the poles (McCulloch *et al.* 1998).

10. Conclusion

Recent mass bleaching events have been correlated with elevated temperatures that act in synergy with light to cause photoinhibition in the endosymbiotic dinoflagellates of hermatypic corals. Photoinhibition acts as a catalyst for a chain of events that results in the dissociation of the cnidarian/algal symbiosis. Lowered temperatures also exacerbate photoinhibition in zooxanthellae, often with a more deleterious effect. In the context of

global climate change, the cumulative impacts of sequential El Niño and La Niña events could have a devastating effect on hermatypic corals. A reduction in the intervals between bleaching events and other natural or anthropogenic disturbances will potentially result in decreased coral cover, reduced species diversity, and changes in community composition. Thus, coral bleaching due to both increased and decreased water temperatures could have globally significant impacts on coral reef communities.

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12. Appendix 1: Photosynthesis

Photosynthesis is a process whereby light energy is converted to chemical energy resulting in the synthesis of reduced carbon, which acts as both an energy source and a building block for other organic compounds (Raven *et al.* 1992; Whitmarsh 1998). It consists of two stages, the light reactions and the dark reactions:

12.1 The light reactions

Light energy is absorbed by pigment-binding proteins that form photosynthetic units called photosystems. Most photosynthetic organisms contain two photosystems that operate in series to oxidise water, reduce NADP^+ and generate ATP (He and Malkin 1998; Morishige and Dreyfuss 1998). Each photosystem is composed of a reaction centre core complex (CC) surrounded by light-harvesting complexes (LHCs) (Raven *et al.* 1992). The LHCs transmit light energy to the reaction centre, acting to increase the absorption efficiency of the photosystem and broaden the absorption spectrum (Morishige and Dreyfuss 1998).

Photosystem I (PSI) and Photosystem II (PSII) are composed of biochemically distinct chlorophyll-carotenoid-binding proteins. In PSI the paired chlorophyll molecules of the reaction centre have an optimal light absorption peak at 700 nanometres, whereas in PSII the optimal light absorption peak is at 680 nanometres. Accordingly, the reaction centre core complexes are called P_{700} and P_{680} respectively (Raven *et al.* 1992). Both photosystems are located in the thylakoids of the chloroplasts, however PSI is mainly found in non-appressed stromal lamellae and peripheral regions of grana, while PSII is mainly found in appressed granal regions (He and Malkin 1998).

The current model of photosynthesis (Fig. 1) proposes that light energy enters PSII, where it is transferred to P_{680} . This energy is absorbed by one of the paired chlorophyll molecules in the reaction centre, boosting one of its electrons to a higher energy level whereby it is transferred to an acceptor molecule. The P_{680} molecule replaces its lost electron by extracting one from a water molecule, which results in the dissociation of water to protons and oxygen gas. This process is known as photolysis. The electron boosted from P_{680} initiates electron flow along an electron transport chain to PSI, resulting in a strong proton gradient that allows the formation of ATP from ADP (photophosphorylation). Meanwhile in PSI, light energy boosts an electron from a P_{700} molecule to ferredoxin, which is then passed through a series

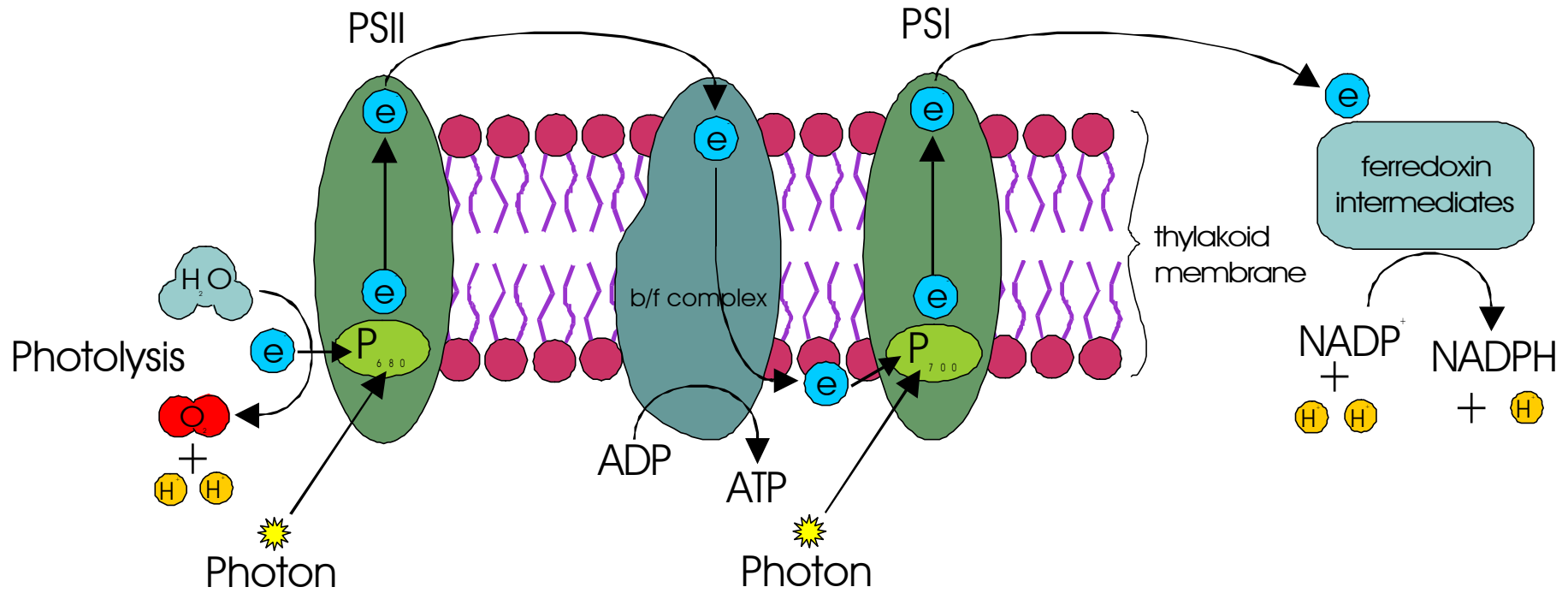


Figure 1: Model of the light reactions. PSII = Photosystem II, PSI = Photosystem I, e⁻ = electron, H₂O = water, O₂ = oxygen, H⁺ = hydrogen, (Adapted from Raven *et al.* 1992; Purves *et al.* 1998)

of intermediates to NADP^+ , which is reduced to NADPH. The electron passed along the electron transport chain from PSII replaces the lost electron from P_{700} . Two photons must be absorbed by both PSII and PSI in order to reduce one molecule of NADP^+ to NADPH (Raven *et al.* 1992; He and Malkin 1998; Morishige and Dreyfuss 1998).

12.2 The dark reactions

The energy captured by photophosphorylation is used to reduce carbon dioxide to simple sugars through a series of reactions known as the Calvin Cycle (Fig. 2) (Raven *et al.* 1992; Sharkey 1998). These reactions occur in the stroma of the chloroplast and are also known as the dark reactions as they do not directly require light (Purves *et al.* 1998). The first step in the cycle is the carboxylation of ribulose biphosphate (RuBP) to produce a 6-carbon intermediate. This initial reaction is catalysed by the enzyme ribulose biphosphate

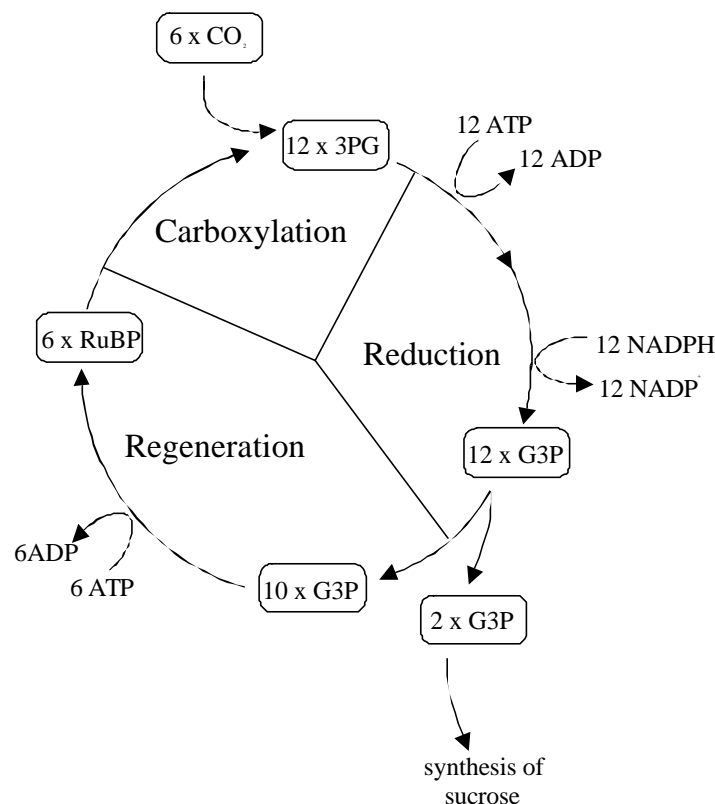


Figure 2: Model of the Calvin Cycle. 3PG = 3-phosphoglycerate, G3P = glyceraldehyde 3-phosphate, RuBP = Ribulose biphosphate, CO_2 = carbon dioxide. (Adapted from Raven *et al.* 1992; Purves *et al.* 1998)

carboxylase-oxygenase (Rubisco). The 6-carbon compound immediately splits to form two 3-carbon molecules, 3-phosphoglycerate (3PG). The second step in the cycle involves the

reduction of 3PG to glyceraldehyde 3-phosphate (G3P) using energy from both ATP and NADPH. From here, two in every twelve G3P molecules are transported to the cytoplasm where they are converted into sucrose, the major transport sugar in plants. The remaining ten G3P molecules are used to regenerate six RuBP molecules, thus completing the cycle (Raven *et al.* 1992; Knox *et al.* 1997; Purves *et al.* 1998; Sharkey 1998).