SYMBIOSIS

VOL. 37, 2004

SYMBIOSIS

AN INTERNATIONAL JOURNAL

VOLUME 37, 2004

BALABAN PUBLISHERS, Philadelphia-Rehovot

Distributed by

International Science Services
POB 2039, Rehovot 76120, Israel
Fax. +972-8-9467632
E-mail. balabanm@netvision.net.il

0334-5114/2004/$05.50

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Comprising selected papers presented at the Fourth International Symbiosis Congress, August 17–23, 2003, Halifax, Canada

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Preface

The field of symbiosis is making a dramatic passage from an interesting but peripheral topic for discussion to a mainstream central tenet of biology. Clear evidence for this are the many high quality and diverse research papers that comprise this volume. They provide insight into just some of the topics presented at the Fourth International Symbiosis Congress held in Halifax, Nova Scotia from the 16th to the 23rd August, 2003, which was attended by 250 delegates from thirty countries.

We appreciate the support of the US National Science Foundation for helping to sponsor the Congress and its follow-up, including travel support for some of the participants. To us, the converted, there is no need to be reminded about the important impacts that symbiosis has upon the formation of the very biomes within which we live. Indeed, symbiosis contributes greatly to the biodiversity of the planet, appears fundamental to understanding evolutionary processes, and influences ecology, medicine, cell research, environmental protection, and agriculture in profound ways. The 4-ISS Congress helped to deepen our understanding and commitment to this growing field.

As members of the International Symbiosis Society, and as subscribers to the *SYMBIOSIS* journal, we have a vehicle, a voice, through which our research visions, findings, ideas and theories can be promoted. Through the Society, we can help focus attention on the whole field of symbiosis which should lead to the greater success of symbiosis-related grant proposals, and to enhanced awareness in the general and scientific community. Our international citizenry needs to appreciate that life survived and thrived on our ancient planet earth via strategies which involved symbiosis including mergers and the integration of very different types of organisms.

This special volume of *SYMBIOSIS* clearly demonstrates the need for greater connections between researchers in different areas of the discipline. We believe that this collection of fascinating papers, peer-reviewed and selected from the latest international symbiosis gathering, will serve as a strong nutrient base that will stimulate further study and a healthy blossoming of the symbiosis field over the coming years.

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0334-5114/2004/$05.50

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Review article.

Coral Reefs in a Century of Rapid Environmental Change

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Received January 28, 2004; Accepted March 8, 2004

Abstract

Coral reefs are the most diverse marine ecosystem and embrace possibly millions of plant, animal and protist species. Mutualistic symbioses are a fundamental feature of coral reefs that have been used to explain their structure, biodiversity and existence. Complex inter-relationships between hosts, habitats and symbionts belie closely coupled nutrient and community dynamics that create the circumstances for "something from nothing" (or the "oasis in a nutrient desert"). The flip side of these dynamics is a close dependency between species, which results in a series of non-linear relationships as conditions change. These responses are being highlighted as anthropogenic influences increase across the world's tropical and subtropical coastlines. Caribbean as well as Indo-Pacific coral populations are now in a serious decline in many parts of the world. This has resulted in a significant reorganization of how coral reef ecosystems function. Among the spectra of changes brought about by humans is rapid climate change. Mass coral bleaching – the loss of the dinoflagellate symbionts from reef-building corals – and mortality has affected the world's coral reefs with increasing frequency and intensity since the late 1970s. Mass bleaching events, which often cover thousands of square kilometres of coral reefs, are triggered by small increases (+1–3°C) in water temperature. These increases in sea temperature are often seen during warm phase weather conditions (e.g. ENSO) and are increasing in size and magnitude. The loss of living coral cover

Presented at the 4th International Symbiosis Congress, August 17–23, 2003, Halifax, Canada

(e.g. 16% globally in 1998, an exceptionally warm year) is resulting in an as yet unspecified reduction in the abundance of a myriad of other species. Projections from general circulation models (GCM) used to project changes in global temperature indicate that conditions even under the mildest greenhouse gas emission scenarios may exceed the thermal tolerances of most reef-building coral communities. Research must now explore key issues such as the extent to which the thermal tolerances of corals and their symbionts are dynamic if bleaching and disease are linked; how the loss of high densities of reef-building coral will affect other dependent species; and, how the loss of coral populations will affect the millions of people globally who depend on coral reefs for their daily survival.

Keywords: Symbiosis, coral, dinoflagellate, global climate change

1. Introduction

Coral reefs are characterized by high levels of biodiversity and complexity. Estimates of the number of species involved in coral reef ecosystems range from 1–9 million with some proposing that only 10% of coral reef species have been described so far (Reaka-Kudla, 1996). Putting their sheer beauty aside, coral reefs are also critical to the survival of at least 100 million people, and to industries that represent billions of dollars of income each year (Bryant et al., 1998). People and industries in these cases depend directly on coral reefs for food and a range of other services including income from fishing and tourism, building materials, coastal protection and new medicines.

Coral reefs are also noted for their high primary productivity in otherwise often nutrient-poor tropical oceans. The extraordinary diversity and productivity generated from so little (i.e. fundamental nutrients that normally underpin ecosystem productivity) has baffled researchers at least as far back as Charles Darwin (Darwin, 1842). Interestingly, the solution to this puzzle appears to lie in the many close symbiotic relationships that are characteristic of coral reefs (Muscatine and Porter, 1977). These linkages frequently involve the close recycling of nutrients and energy (Muscatine and Porter, 1977; Hatche, 1988), which means that the primary producers and consumers on coral reefs avoid the problem of the dilution of nutrients and food in the clear waters of the tropics. This phenomenon occurs at different scales ranging from those of endosymbiotic associations (e.g. Trench, 1979) and close ecological associations (e.g. Odum and Odum, 1955; Meyer and Schultz, 1985) to features of the large-scale reef matrix that trap water and hence allow the further recycling of nutrients and particles (Richter et al., 2002).

Estimates of the gross primary productivity of coral reefs range from 2.3 to 6.0 $gC.m^2.d^{-1}$, depending on the location of particular reef ecosystems (Hatcher,

1988) and local conditions (Kleypas et al., 1999). Coral reefs decrease in abundance and vigor at higher latitudes, primarily as a function of decreased light, temperature and aragonite saturation. In circumstances where coral reefs have formed along coastlines in which rivers dump sediments and nutrients from the land, light levels may diminish rapidly with depth as turbidity increases. In these cases, coral reefs may have lower primary productivities and grow to shallower maximum depths than coral reefs that grow in the clear waters characteristic of offshore sites. The diversity of species associated with coral reefs (as with almost all other ecosystems) also decreases toward the poles. Species diversity may be two orders of magnitude less at high latitudes than at lower latitudes (Veron, 2002).

Coral reefs appear to be extraordinarily sensitive to changes in the environment that surrounds them (Wilkinson and Buddemeier, 1994; Brown, 1997; Hoegh-Guldberg, 1999). These changes to the conditions under which corals have prospered are occurring rapidly with estimates of the loss of 30% of coral populations since the 1980s (Wilkinson, 2000) and future losses of between 30–90% of coral dominated reefs by 2050 (Wilkinson and Buddemeier, 1994; Hoegh-Guldberg, 1999). Among the changing conditions surrounding corals are changing levels of coastal sediment and nutrient run-off, fishing and harvesting and global climate change. These changes affect organisms within coral reef ecosystems directly (Hoegh-Guldberg, 1999), or indirectly by modifying ecosystem function (Jackson et al., 2001; Pandolfi et al., 2003) and have already resulted in major changes in the distribution of corals and the organisms that live in and around them (Hughes, 1994; Bryant et al., 1998). The exponential increase in people inhabiting coastal areas immediately adjacent to coral reefs continues to drive up the pressure on coral reefs. People living along coastlines have escalated land run-off, fishing pressure and resource use. This, in addition to increasing greenhouse emissions primarily from developed societies such as the United States, Europe and Australia, has amplified the pressures being experienced by coral reefs (Hughes et al., 2003).

An in depth discussion of the entire spectrum of the changes being exerted on coral reefs is beyond the scope of this review, which focuses primarily on the mutualistic symbiosis between corals and dinoflagellates, and the influence of a rapidly changing climate. This particular example of mutualism is important because it underpins the physiology of the so-called framework builders of coral reefs (reef-building corals). After examining our current understanding of corals and their unique symbionts, the current and future challenges that face corals and the reefs they build will be briefly reviewed. In doing so, climate change emerges as the most serious threat to the integrity of these symbioses and hence the highly productive and diverse nature of coral reef ecosystems. While climate change may be the most serious threat, action to counter its effects involves a wider spectrum of changes to the way we interact with coral reefs. As will be argued, reducing other more local threats is important and has to work hand in hand with any strategy aiming to deal with the impacts of a rapidly changing climate.

2. Phototrophic Mutualism in Tropical Seas

The close association of primary producers and consumers is a major feature of life in tropical oceans. Table 1 lists several of the prominent examples on coral reefs. In the broadest sense, plant-animal symbioses range from the association of prokaryotes and the simplest animals (sponges) to those involving single-celled eukaryotes and complex animals such as clams and gastropods. Other associations (though not mutualistic *sensu stricto*) involve the acquisition of chloroplasts (kleptoplasty) that are removed from the tissues of plants and integrated into the tissues of an animal host.

Phototrophic associations are built on the advantages gained from the internalized exchange of photosynthetic products and inorganic nutrients (Trench, 1993). Most of the associations involve endosymbiotic associations where the plant resides within vacuoles in the cells of the animal host with the noticeable exceptions of Tridacnid clam, sponge and tunicate symbioses. In these cases, the phototroph resides outside the host cells in specialized host compartments or channels (Norton et al., 1992; Lewin and Cheng, 1989).

Table 1. Examples of phototrophic mutualistic symbioses involving animal hosts on coral reefs together with representative literature.

Phototroph	Host(s)	Reference
Prochloron	Diademnid tunicates	Lewin and Cheng (1989)
Cyanobacteria	Sponges	Hinde et al. (1994); Wilkinson (1978, 1987); Diaz and Ward (1999)
Dinoflagellates	Foraminiferans, sponges, corals, flatworms, clams, nudibranchs	Trench (1979, 1981, 1987, 1993); Taylor (1971); Kempf (1984); Rudman (1982, 1987); Hoegh-Guldberg et al. (1986); Lee and Anderson (1991); Norton et al. (1992); Hallock (2000)
Chloroplasts of green and red algae	Saccoglossan molluscs	Green et al. (2000); Rumpho et al. (2000)
Red and green algae	Sponges	Simpson (1984); Trautman et al. (2000); Davy et al. (2002)

3. Coral-Dinoflagellate Mutualistic Symbiosis

One of the most prominent phototrophic mutualistic symbioses on coral reefs involves the association of dinoflagellates (*Symbiodinium* spp) with both Scleractinian and Alcyonacean corals (Fig. 1). These organisms reside within the cells of endodermal cells that line the gastrovascular cavity of the host. The mutualistic association of coral and dinoflagellates has been the subject of much interest since the realization that the brown cells of many invertebrates were separate organisms (Brandt, 1881). Symbiotic dinoflagellates live in the tissues of hundreds of species of cnidarians as well as animals from at least four other phyla including Mollusca (snails and clams), Platyhelminthes (flatworms), Porifera (sponges) and Protista (e.g. single-celled ciliates, Foraminifera). Their lifecycles include motile free-living stages that undergo sexual reproduction (Baillie et al., 2000; Goulet and Coffroth, 2003).

Within these organisms, *Symbiodinium* loses the characteristic biflagellate and sculptured structure of a motile dinoflagellate and assumes a cocoid non-motile form. The lack of distinct features of the cocoid symbiotic stage led early taxonomists to ascribe most dinoflagellates living in invertebrate hosts to a single species, *Symbiodinium microadriaticum* (Freudenthal, 1962; Taylor, 1968). Robert Trench and co-workers (Trench, 1979; Schoenberg and Trench, 1980a, 1980b; Rowan and Powers, 1991) demonstrated, however, that *S. microadriaticum* included many taxa that were structurally, physiologically and genetically distinct from each other (Fig. 2). A number of broad phylotypes has now been identified using a range of markers (18S rDNA, 28S rDNA and ITS regions particularly). These have been assigned letter codes (A-C; Rowan and Powers, 1991) and appearing to represent taxa at least at the genera level (Banaszak et al., 1993). Further investigation has concluded there are at least seven genera of dinoflagellates which belong to as many as four orders (Banaszak et al., 1993; Santos et al., 2002).

Recent work (reviewed in this volume by LaJeunesse) reveals diversity at even finer scales using the intron spacer, ITS2. At these levels, a single reef such as Heron Island on the southern Great Barrier Reef, may have over 20 different phylotypes (ITS2) among just 86 host species (LaJeunesse et al., 2003, see complete list in the web resource at http://www.aslo.org/lo/toc/volp48/issuep5/2046al.pdf). *Symbiodinium* taxa vary geographically within and between hosts. Coral hosts may also form symbioses with different genetic varieties of *Symbiodinium* in different parts of their distribution. *Seriatopora hystrix* (Scleractinia) has C phylotype of *Symbiodinium* when collected from southern Great Barrier Reef or Japan yet type D phylotypes when collected in Malaysia (Loh et al., 2001). Similar observations can be made for the geographically extensive coral *Plesiastrea versipora*, which is has phylotype C in most low latitude Australian populations but has phylotype B at high

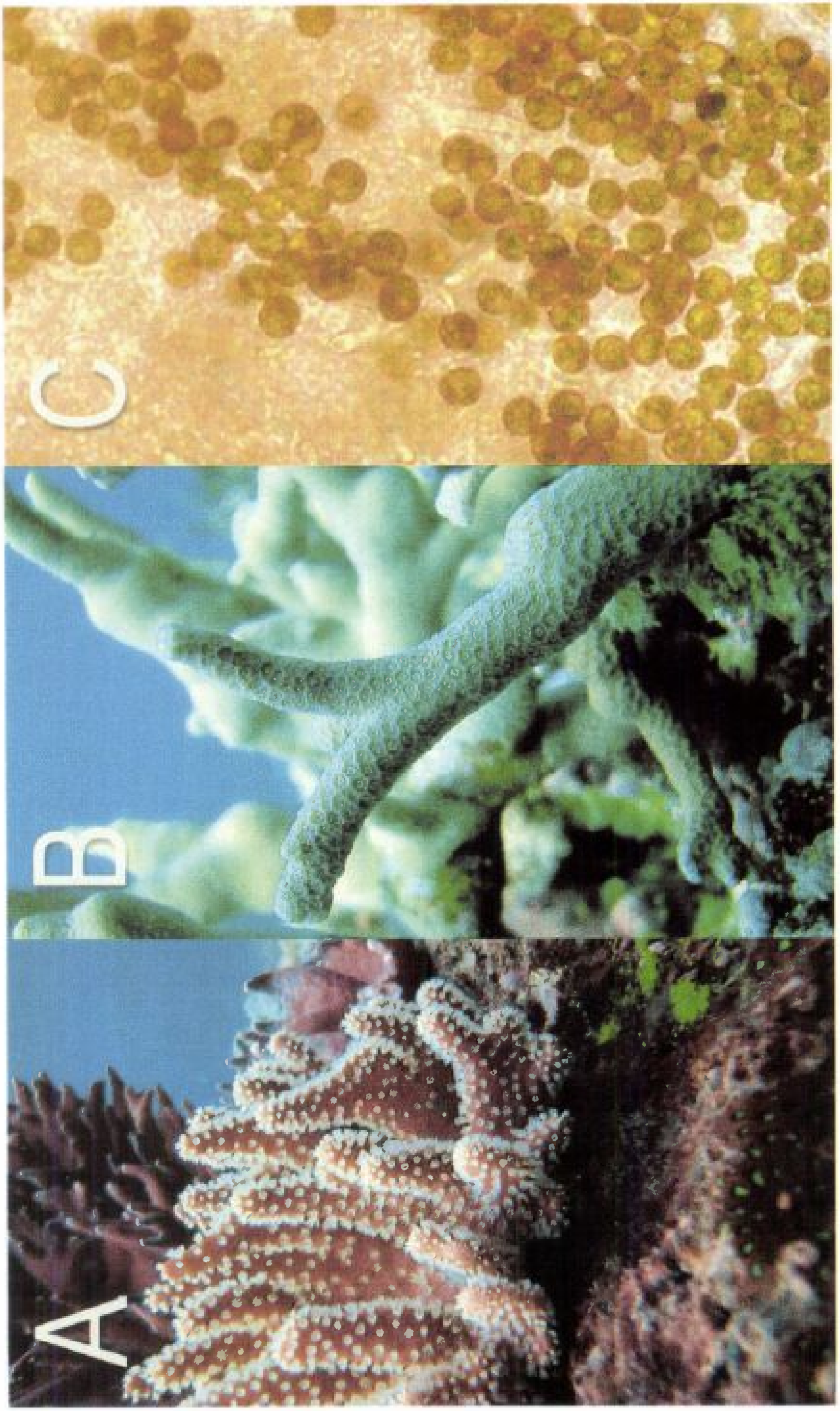

Figure 1. See legend on next page.

latitude locations (Rodriguez-Lannetty et al., 2001). Major differences have also been observed at the sub-cladal level between Caribbean and Pacific corals, which only share a small number of *Symbiodinium* genotypes (putative generalists C1 and C3; LaJeunesse et al., 2003).

Corals may also include a variety of *Symbiodinium* taxa within the one host species. *Montastraea annularis* and *M. faveolata* from the Caribbean can contain multi-species assemblages of *Symbiodinium* within single hosts (Rowan et al., 1997). Similar observations have been made for other coral species (Loh et al., 1998; 2001; Baker, 2001a; LaJeunesse, 2001, 2002; LaJeunesse et al., 2003). While not the rule (many coral taxa appear not to include more than one phylotype) multicladal communities of dinoflagellate symbionts probably engender ecological flexibility that may be significant in extending the range of species either within a site (e.g. Baker, 2001a) or geographically (e.g. Rodriguez et al., 2001). A full understanding of how the genetic diversity of *Symbiodinium* influences the physiology and ecology of reef-building corals and other hosts is its infancy. While it is clear that some genotypes may confer distinct physiological and ecological advantages on their hosts, it is unclear whether this is always the case. It is also possible that distinct infection events in evolutionary history may have lead to different genotypes converging evolutionarily on a similar physiological form. That is, the genetic differences between *Symbiodinium* within a host or even between host species may not represent *Symbiodinium* phylotypes that are different physiologically or ecologically (Hoegh-Guldberg et al., 2002).

Resident symbiotic dinoflagellates capture light and process it at rates that match free-living or cultured cells (Muscatine, 1990). Symbiotic dinoflagellates differ from free-living single-celled algae, however, in that they translocate up to 95% of their photosynthetic production to the host (Muscatine, 1967, 1990), principally as amino acids, sugars, complex carbohydrates and small peptides (Muscatine, 1973; Trench, 1979). In return, corals (by way of on-going catabolic processes) provide critical inorganic nutrients (e.g. ammonia and phosphate) to their intracellular residents (Trench, 1979). This exchange sits at the heart of the mutualistic symbiosis that binds corals and their dinoflagellates together, and makes possible the framework of coral reefs in the often nutrient-poor tropical oceans.

See figure on previous page.

Figure 1. Both A. soft corals (shown is *Lobophytum* sp., subclass Octocorallia, order Alcyonacea) and B. hard corals (shown is *Porites nigrescens*, subclass Hexacorallia, Order Scleractinia) form mutualistic symbioses with C. *dinoflagellates* of the genus *Symbiodinium*. Photographer: Ove Hoegh-Guldberg.

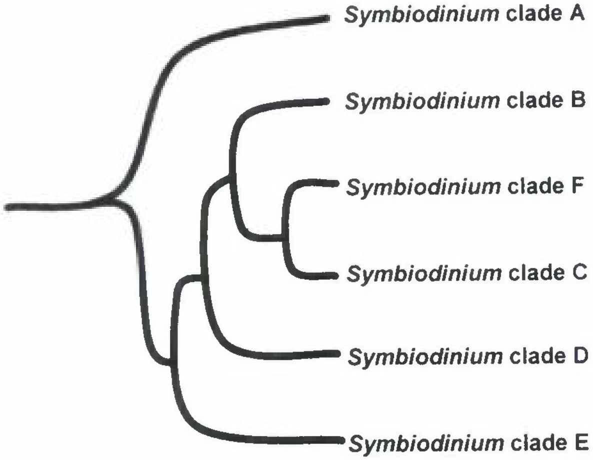

Figure 2. Phylogenetic relationships between the major clades of *Symbiodinium* derived from 5.8S ribosomal DNA. Redrawn from LaJeunesse (2001).

The abundant energy supplied by *Symbiodinium* to their host corals powers the precipitation of calcium carbonate, allowing corals to build the limestone reefs that have dominated the Earth's tropical waters for hundreds of millions of years. These structures are cemented together due by organisms such as calcareous red algae and are populated by millions of species of plant, animal, protist and prokaryote life forms. The energy trapped by corals and other phototrophs on coral reefs down a complex web (Odum and Odum, 1955) which provides the basis for the most diverse of the Earth's marine ecosystems. Marine bird, reptile and mammal populations can often be impressive in size in the islands and coastlines associated with coral reefs. Historically, populations at these upper trophic levels were even larger (Jackson et al., 2001; Pandolfi et al., 2003).

4. Coral Reefs in a Time of Change

Recent assessments of the health and abundance of coral reefs reveal a worrying decline (Bryant et al., 1998; Wilkinson, 2000). Examination of recent tends suggest that approximately 30% of the world's reefs have been effectively lost over the past 3 decades (Wilkinson, 2000). Projections of future losses from human derived stresses (excluding climate change, see discussion below) range up to a staggering 60% of today's coral reefs being lost by 2030

(Wilkinson, 2000). The reasons for the declining health of coral reefs lies in a broad spectrum of human activities which are tied explicitly to the steady and rapid rise in human populations and their use of resources at both a global scale and along coastlines bordering coral reefs. Rising human population numbers along tropical coastlines has led to major changes in the state of ecosystems from the following activities:

Coastal development

The expansion and intensification of urban centres, roads and agricultural activity have dramatically increased the levels of nutrients, toxins and sediment entering coastal areas adjacent to coral reefs. These changes have been implicated in stimulating the overgrowth on inshore coral reefs by macroalgae, causing coral mortality and setting off population outbreaks of potential coral predators such as the Crown-of-Thorns Starfish, *Acanthaster planci* (e.g. Bryant et al., 1998; McClanahan et al., 2002; Koop et al., 2000; Harborne et al., 2001).

Overexploitation of key functional groups with coral reefs

The increasing numbers of people in the coastal zone has led to rapid increases in fishing pressure by local subsistence fishers. Additionally, the global demand for fresh seafood has stimulated a large rise in the intensity and geographic extent of fishing industries (Hughes et al., 2003). As a result, most fish stocks in tropical as well as temperate oceans are in major decline and most have fallen to less than 10% of the previous unexploited abundance (Meyers and Worm, 2003; Boersma and Parrish, 1999). The removal of fish leads to a loss of functional groups (herbivores, predators) that are important to controlling other organisms within the ecosystem. Widespread ecological changes have also resulted from the elimination from these key ecological groups from coral reefs (e.g. Hughes, 1994; Jackson et al., 2001; Pandolfi et al., 2003).

Destructive fishing

The techniques used to catch fish are having major impacts on coral reefs. In many places, local fishers resort to dynamite or cyanide fishing as fish stocks drop to low levels due to fishing pressure. Trawling for prawns and other coastal organisms is also destroying key habitats associated with coral reefs. These activities are continuing to cause the localized destruction of coral reefs and the organisms that grow on them (Jones and Hoegh-Guldberg, 1999; Jones et al., 1999; McClannahan, 1999; McClannahan et al., 2002a; Edinger et al., 1998). In some regions (e.g. SE Asia, Bryant et al., 1998), destructive fishing is considered to be the most serious short-term threat to the integrity of coral reef ecosystems.

Marine-based pollution

Chemicals dumped by shipping (anti-foulants) have a direct effect by poisoning or smothering (e.g. oil spills) corals and associated organisms. Incidents involving shipping are increasing as are associated activities (e.g. trash, ghost nets; Bastidas et al., 1999; Abelson et al., 1999; Edinger et al., 1998). Due to the growth of shipping globally, this problem has assumed major proportions across vast sectors of the tropical oceans that contain coral reefs.

Climate change

Rising sea temperatures and decreasing aragonite saturation states are changing the conditions under which coral reefs have prospered for at least 400,000 years. Since 1979, there have been six major global episodes of mass coral bleaching. These events have increased in frequency and intensity over the past two decades and are caused by sea temperatures rising 1–3°C above long-term summer maxima. These global events are due to rising global temperatures (Glynn, 1991; Goreau and Hayes, 1994; Hoegh-Guldberg and Salvat, 1995; Hoegh-Guldberg, 1999), which have increased tropical sea temperatures by as much as 1–2°C over the past century (Hoegh-Guldberg, 1999; Lough 2000, 2001). As will be argued below, these changes lead to predictions in which the prospects for coral dominated reef systems anywhere on the planet by 2050 appear minimal.

The various threats listed above do not operate in isolation. Important synergies clearly operate between the various forms of human influence on coral reefs. This point should be kept in mind in the following discussion, which will explore the current and future impacts of the earth's changing climate on coral reefs. The discussion will now focus on climate change for two reasons. The first is that it is considered by many researchers today to be the largest threat to the health of coral reefs and the many people that depend on them (Done et al., 2003; Kleypas et al., 2001) and secondly, it has the potential to exacerbate the many other threats facing coral reefs through interactions and synergies (Hoegh-Guldberg, 1999; McClannahan et al., 2002b; Hughes et al., 2003). Understanding the reasons for the decline of coral reefs due to climate change and how these interactions might develop is critical to our response to global climate change over the next fifty years.

5. Coral Bleaching, Mortality and Recent Global Change

Symbiotic dinoflagellates are not constant in their behaviour and vary both their physiology and population densities in response to seasonal changes in environmental conditions (Jones, 1995; Fagoonee et al., 1999; Fitt et al., 2000). Symbiont cell number, host tissue thickness and the concentration of photosynthetic pigments per dinoflagellate cell shift seasonally, probably to optimize the performance of the coral-algal symbioses as conditions change. Abrupt decreases in the population density of symbiotic dinoflagellates within invertebrate hosts occur in response to rapid or stressful changes to the physical and chemical environment surrounding the association. These changes include variation to salinity (Goreau, 1964; Egana and DiSalvo, 1982), photosynthetic radiation (low and high: Vaughan, 1914; Yonge and Nichols, 1931; Hoegh-Guldberg and Smith, 1989; Jones et al., 1998), ultraviolet radiation (Gleason and Wellington, 1993; Lesser et al., 1990), toxins (e.g. cyanide, Jones and Hoegh-Guldberg, 1999; copper ions Jones, 1997; diuron and atrazine, Jones et al., 2003), microbial infection (e.g. Vibrio, Kushmaro et al., 1996) or temperature (high: Jokiel and Coles, 1977; 1990; Coles and Jokiel, 1978; Hoegh-Guldberg and Smith, 1989; Glynn and D'Croz, 1990; low: Saxby et al., 2003).

In contrast to the more gentle seasonal changes, these changes may lead to a massive reductions of the brown pigments associated with symbiotic dinoflagellates, a syndrome referred to as bleaching (Fig. 3).

Bleached corals may recover or die, depending on the intensity and longevity of the stress and the interactions with other more local factors. Concentrations of dinoflagellate symbionts may increase in bleached corals with time if the initial stress is not too prolonged or severe. The recovery of symbiont populations results from the growth from symbionts that remain in the tissues even when corals are bleached (Hoegh-Guldberg and Smith, 1989; Goulet and Coffroth, 2003). If, on the other hand, stresses are prolonged or elevated, bleached corals may die (Glynn, 1993; Brown, 1997). In these cases, death may be a direct consequence of either the stress itself or the result of opportunities given to other organisms that either invade coral surfaces (disease organisms or surface microalgae) or out compete them (macroalgae).

There have been six major periods of mass coral bleaching reported in the scientific literature since 1979 and none prior. During these global scale events, several entire regions (e.g. Great Barrier Reef, Western Indian Ocean) have bleached within months of each other. The global events of 1997–98 dwarf all previous impacts, with bleaching being reported in most coral reef regions over a 12 month period. The resulting mortality was also high in some regions over others (Table 2).

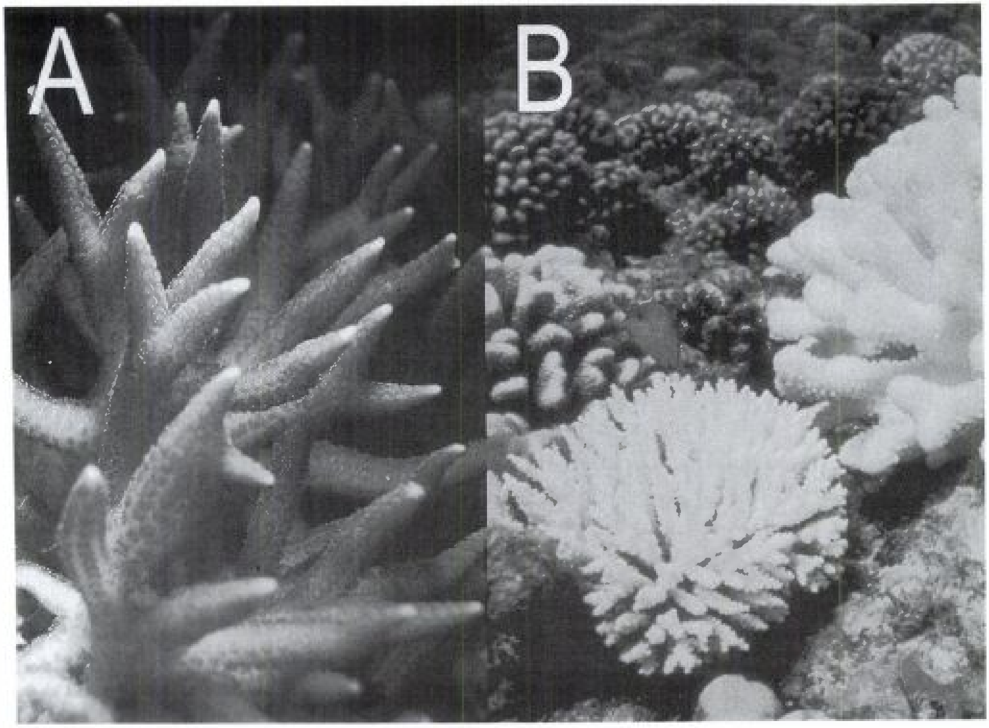

Figure 3. A. Reef-building corals (in this case, *Seriatopora hystrix*) have an overall brown colour due to their abundant symbiotic dinoflagellates. Photographer: Ove Hoegh-Guldberg. B. Stressed corals often loose their dinoflagellate symbionts and turn a brilliant white (bleach). Shown are bleached colonies of *Acropora* sp. (front) and *Pocillopora verrucosa* (right). Photographer: Roger Grace.

Table 2. Percent decrease in the areal cover of reef-building corals from 1997 to 1998. (Adapted from Wilkinson, 2000).

Region	% Change in surveys (from 1997 to 1998)
Arabian Region	33
Wider Indian Ocean	46
Australia, Papua New Guinea	3
Southeast & East Asia	28
Wider Pacific Ocean	5
Caribbean Atlantic	1
Regional average	16

In the Indian Ocean, for example, living coral cover decreased by 46% over the 12 month period. Many of these regions have yet to significantly recover. Other regions, however, were far less affected. Australia and Papua New Guinea, by contrast, suffered an average loss of only 3% during the same period. These comments must also be tempered with the fact that corals that survive a bleaching event are not necessarily unaffected. Corals at Heron Island, for example, mostly survived the 1998 bleaching event yet had reduced spawning for at least two years later (Ward et al., 2001). As symbionts provide the key energy resource for growth, calcification and reproduction, it is not surprising that bleached corals grow, calcify and reproduce less (Goreau and Macfarlane, 1990; Leder et al., 1991; Szmant and Grassman, 1990; Ward et al., 2001; Michalek-Wagner and Willis, 2001).

Historically, global sea temperatures have increased by approximately 0.6–1.0°C over the past 100 years (Collins and Della-Marta, 1999; Lough, 2000, 2001). Sea temperatures in northern Australia (including the Great Barrier Reef), for example, have increased by up to 0.1°C per decade over the past 100 years (Lough, 2000). These changes have brought reef-building corals and their symbiotic dinoflagellates closer to their upper thermal tolerances. In some parts of the world, rates of change may even be higher. The research station at La Parguera in Puerto Rico, for example, has registered a rate of change of 2.53°C per century (Winter et al., 1998), while Brown (1997a) reports a increase in sea temperature (using MOHSST 6 data going back to 1946) of 1.26°C per century (Brown, 1997a). Most studies of the change in sea temperature over the past century reveal rapid change relative to even the most rapid periods of change in the past several thousand years (Hoegh-Guldberg, 2003).

Mass coral bleaching events are almost entirely explained by periods of increased sea temperature in which the thermal threshold of reef-building corals and a wide range of other symbiotic invertebrates is exceeded (Hoegh-Guldberg, 1999). Thermal thresholds decrease in a poleward direction as a result of the evolutionary adaptation of reef-building coral communities to the lower sea temperatures of these regions (Coles et al., 1976; Hoegh-Guldberg, 1999). As discussed elsewhere, the causal association of mass coral bleaching with elevated sea temperatures is indicated by the predictive success of the HotSpot program run by the National Atmospheric and Oceanographic Administration (NOAA; http://www.osdpd.noaa.gov/PSB/EPS/SST/climohot.html). This program can predict coral bleaching by as much as weeks in advance by simply measuring the intensity and duration of positive thermal anomalies. These field based observations and predictions are also reinforced by the numerous experimental studies that have replicated the symptoms of mass coral bleaching using thermal stress conditions that are similar to those that occur during mass bleaching (e.g. Jokeil and Coles, 1977; Hoegh-Guldberg and Smith, 1989; Glynn and D'Croz, 1990).

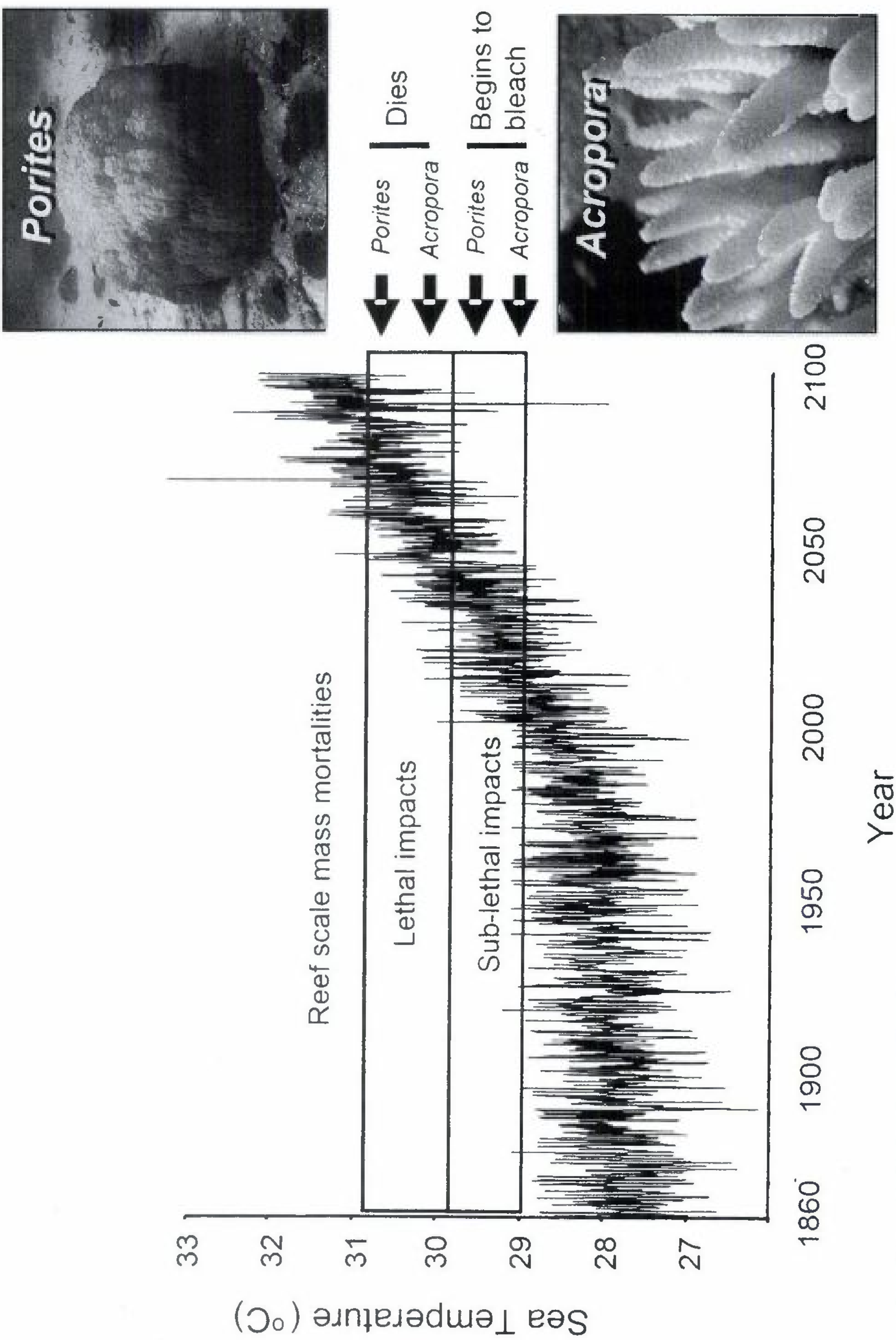

Figure 2. See legend on next page.

From these studies mechanistic models have been developed that reveal similar if not identical biochemical processes to those occurring in heat-stressed higher plants (Bilger et al., 1987; Iglesias-Prieto et al., 1992; Warner et al., 1996; Jones et al., 1998; Salvuccia and Crafts-Brandnera, 2004). These mechanistic models also explain why light (as Photosynthetically Active Radiation "PAR") exacerbates the effect of heat on corals (Jones et al., 1998).

6. Projections of Change on Coral Reefs

Changes in sea temperature over the past century explain the advent in 1979 and the resulting increasing frequency and intensity of mass bleaching events over the past two decades (Hoegh-Guldberg, 1999). The simple relationship between elevated temperature and mass coral bleaching can also be combined to produce simple projections of how the frequency and intensity of mass bleaching events are likely to change as climate change continues to occur (Fig. 4).

Some species have greater thermal tolerances than others with the genera such as *Porites* being far more resistant to bleaching than corals from the genus *Acropora* (Hoegh-Guldberg and Salvat, 1995; Loya et al., 2000). These differences also translate into differences in terms of the threshold at which mortality starts to become significant. These differences between corals translate as a range of thermal tolerances within a reef that may be up to 1°C different. Corals may also differ between individuals within a species in terms of thermal tolerance. In these cases, a combination of genetic and phenotypic influences (Brown, 1997; Brown et al., 2000; Coles and Brown, 2003) probably go into determining the slight differences seen between the thermal response of individuals within a coral species.

Projections under even the mildest climate scenarios (e.g. IS92A, Hoegh-Guldberg, 1999) reveal that tropical sea temperatures are set to rise annually above the thermal threshold for coral bleaching and mortality within the next

See figure on previous page.

Figure 4. General circulation model data for tropical sea temperatures associated with a typical Pacific coral reef at latitude 15°S. Model data were generated using ECHAM4-OPC3 (Roeckner et al., 1996, provided by Dr Axel Timmermann of KNMI, The Netherlands; aerosol effect included). A range of thresholds exist for a community of corals, some corals such as *Porites* sp. (insert) are slightly more tolerance to thermal stress than less massive genera such as *Acropora* (insert). Beyond an upper temperature, however, entire communities of corals will bleach and eventually die. As temperatures keep rising, entire communities and reefs will become vulnerable to mass mortalities.

30–50 years. Recent work by Strong and others has revealed that projections are significantly improved if the exposure time is considered along with anomaly size. This technique which calculates Degree Heating Weeks (or Degree Heating Months, DHM) is currently being used to accurately project the outcome of thermal events occurring today (Strong et al., 2000). Back-calculated DHM values from the events of 1997–98, for example, reveal that events that resulted in mass mortalities that exceeded 80% of the reef-building corals at a location (e.g. Okinawa, Seychelles, Palau, Scott Reef) experienced DHM values of 3.2 + 0.47 while those with low or zero mortality had DHM values of 1.1 + 0.49 (Hoegh-Guldberg and Hoegh-Guldberg, 2004). That is, the difference in outcome with respect to mortality can be tracked to whether a region 1°C or 3°C increases over a month (1°C for 1 or 3 months in duration) in sea temperature over long-term summer sea temperatures.

DHM values can be used to improve our understanding of how coral reefs might be affected by future changes in sea temperature. Under a doubling of atmospheric carbon dioxide by 2100, DHM values for reefs at 12 sites in the Pacific Ocean steadily until thermal stress on reefs is 5–10 times greater than the thermal stress was seen in the worst affected areas of 1998 (Hoegh-Guldberg, 2001). If these approaches are combined with the observation that DHM values over 3.2 are associated with major mortality events, an understanding of the frequency of major bleaching and mortality events in the future can be gained (Fig. 5).

Logically, if total mortality events that occur more than 3 times per decade, reefs under this type of stress that will no longer be dominated by corals. This is supported by the observation that reefs like those of Palau, NW Australia and Okinawa have not recovered fully from the 1997–98 mass bleaching event. Wilkinson (2002) highlights this in the Executive summary of the latest Global Coral Reef Monitoring Network assessment of coral reefs world-wide in relation to the reefs showing the fastest signs of recovery since the last global mass bleaching event "There has been considerable recovery in the unstressed reefs of Southeast and East Asia and Palau, and also along the Great Barrier Reef of Australia, but it will take several decades before reefs return to pre-1998 status. There is broad concern that another Climate Change/El Niño event could arrest the recovery."

The overwhelming conclusion however is that mass mortality events like those of Palau, Scott Reef and Okinawa cannot occur every 3–4 years without eventually bringing coral populations to close to zero. This assumption is probably highly conservative given that the anomaly size continues to grow (>>3.2 DHM) in addition to the frequency.

The conclusions of these approaches to understanding the future are striking. If reef-building corals and their symbionts do not change their thermal

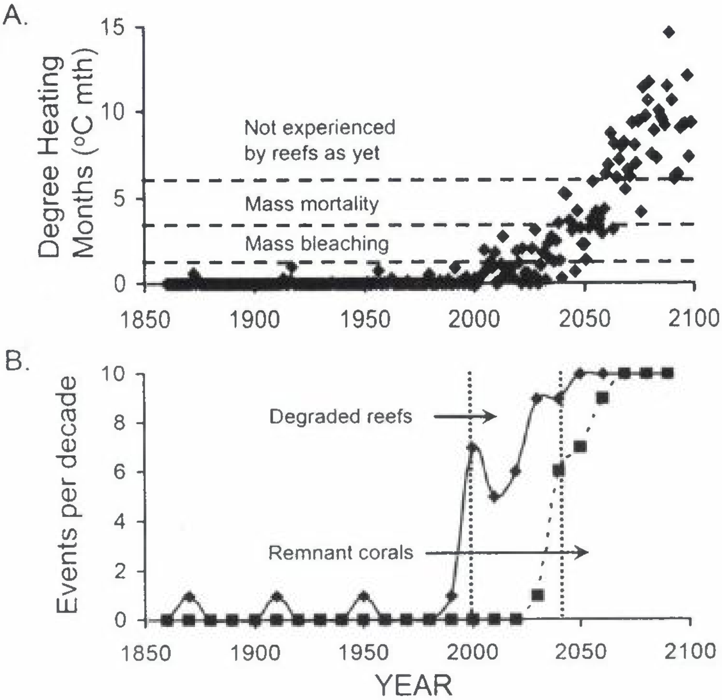

Figure 5. Projected changes to the heat stress and resulting rates of mortality for corals growing on the central Great Barrier Reef. Data were calculated generated using the ECHAM4-OPC3 general circulation model (Roeckner et al., 1996, provided by Dr Axel Timmermann of KNMI, The Netherlands; aerosol effect included). A. Shows the accumulated heat stress values (as Degree Heating Months or DHM) which are simple multiples of the extent to which temperatures exceed thresholds multiplied by the time that they are above the thresholds. B. The frequency of bleaching events per decade over the next century (DHM>1.0, dotted line) and severe events (DHM>3.2, second dotted line). Events that rise above 6.0 have never been experienced by coral reefs in recent history. When coral reefs experience bleaching events every two years, reefs are expected to degrade (indicated by arrow). When severe mortality events (when DHM>3.2) are experienced every two years, coral populations are expected to be remnant as mortality grossly exceeds recovery.

tolerance (see discussion below), then rapid increasing sea temperatures will increase the chance of mass mortality events (years with DHM values of 3.2 or more) until they are more or less annual events by the middle to end of the current century. Using the criteria established above, reefs will shift to non-coral dominated states by 2020 in Jamaica, 2030 in Phuket and 2050 in Tahiti (Hoegh-Guldberg and Hoegh-Guldberg, 2004).

These issues have also been discussed by Done et al. (2003) in which probabilities are assigned to the ecological impacts on coral reefs of thermal stress events that range from mild to catastrophic. Under even the best case scenarios, the likelihood of a 'catastrophic' exposure (>100 days of elevated sea water temperatures; DHM values >>3) is at least 10% for the mid and offshore reef sites (see Fig. 22 in Done et al., 2003). This is essentially the same as saying that catastrophic events (major mortalities reaching up to 100% of all corals in an area) are highly likely every 10 years by this point. Given that reefs (as discussed above) take at least 15–30 years to recover depending on local conditions (Done et al., 2003), reefs are likely to have very low coral cover if impacted every 10 years by total wipe-out events. Important in this analysis is to realize that the years in between catastrophic events are populated by more regular events that may have large effects on reefs themselves. Reefs are unlikely to be dominated by corals under these climate regimes.

7. Critical Assumptions: Rates of Adaptation versus Climate Change

Critical to the analysis presented above is relative stationary nature of the thermal thresholds of reef-building corals and their symbiotic dinoflagellates. Theoretical additions of high rates of adaptation to these models lead to more optimistic outcomes from the above analysis (Hoegh-Guldberg, 2001; Done et al., 2003). Critical evidence, however, for ability of corals to rapidly change their thermal thresholds within ecological time scales is scant at best. It is apparent, for example, that thermal thresholds differ between geographical locations (Coles et al., 1976; Hoegh-Guldberg, 1999; Coles and Brown, 2003) indicating, not surprisingly, that reef-building coral associations adapt to the local thermal conditions. The issue, however, is how fast these genetically based changes in thermal threshold occur (Hoegh-Guldberg, 1999) – past adaptive changes took hundreds if not thousands of years to occur. This remains the critical issue, highlighted by the fact that the rapid warming after glacial periods over the past 400,000 years was much slower than current rates of warming yet still resulted in major biological shifts and extinctions.

Coles and Brown (2003) recently claim that issues of the variability of coral responses to thermal stress have been missed within studies that project of how corals will respond to a rapidly changing climate. This perspective is at odds with the often lengthy discussion of the issue of acclimation and adaptation in the same papers (e.g. Hoegh-Guldberg, 1999). Clearly, the acclimation and adaptation issue is very important and Coles and Brown (2003) provide a thorough review of the many mechanisms that have been discovered recently within corals and their dinoflagellates in order to cope with changes in the environment. These mechanisms, however, have their limits. Clearly the rapid increase in coral mortality (e.g. 46% coral mortality of Indian Ocean corals, Wilkerson, 2000) in relation to the rising thermal stress of the past three decades is strong evidence that acclimation and adaptation are not potent forces at the current time scale of change. Even quoting optimistic statements as do Coles and Brown (2003, the "potential for greater physiological tolerance than might have been previously expected", Done, 1999) adds very little to the discussion unless firm hard data are presented to show that changes in response are occurring and that genetic change has the potential to keep up with the extremely rapid pace of environmental change.

Recently, Glynn and co-workers have attempted to detect the adaptation by reef-building corals to thermal stress to the changes in ocean temperature in the Eastern Pacific. These workers have noted that the impact of the 1997–98 event on coral populations was smaller than the impact of the 1982–83 event, even though the size of the thermal anomaly was equal to or greater in 1997–98 than in 1982–83 (Glynn et al., 2001). The authors suggest that the reason lies in the 1998 population having become more thermally tolerant due to the selection of more tolerant individuals in the earlier event. Data that demonstrate, however, that stress levels were identical or increased in 1998 are not convincing. The environmental conditions that determine how much bleaching and mortality occur, for example, do not depend on temperature alone. Mumby et al. (2001) revealed that cloudiness can significantly decrease the effect of thermal stress as predicted by physiological models of bleaching (Jones et al., 1998). In their study, Mumby et al. (2001) note that much less coral bleaching occurred around Tahiti and Moorea in 1998 than was expected from the calculated exposure to thermal stress. Comparison with previous bleaching events in the same area, however, revealed that 1998 was unusually cloudy and that this probably led to lower levels of stress (as predicted by the model of Jones et al., 1998). Glynn et al. (2001), in relying almost solely on sea temperature data, cannot rule out that differences in response by corals were not due to differences in cloudiness or other aggravating factors that might change the amount of stress being experienced by corals in the two events. Without these data, it is not possible to conclude that Eastern Pacific corals in 1998 were less sensitive to thermal stress than they were in 1983.

Changes in thermal thresholds might also occur if reef-building corals were able to swap their dinoflagellate symbionts for more thermally tolerant varieties (Baker, 2001b). Buddemeier and Fautin (1993) have suggested the intriguing possibility that coral bleaching might be a "adaptive" mechanism by which corals rid themselves of thermally sensitive dinoflagellates and replace with new varieties from the external environment that are more thermally tolerant. If true, the Adaptive Bleaching Hypothesis (ABH) hypothesis would allow for the rapid evolution as long as symbionts with greater thermal tolerance were available in the environment surrounding reef-building corals. Unfortunately, evidence for bleaching resulting in the swapping of symbionts during bleaching is at best equivocal. Baker (2001b), for example, observed a change in the major dinoflagellate phylotype found in corals that were moved from deep water to shallow water. The molecular techniques used in the study, however, are unable to detect whether the new phylotypes (using Restriction Fragment Length Polymorphism or RFLP) were already present in the corals prior to being stressed and bleached or if they were new comers to the association (Hoegh-Guldberg et al., 2002). This distinction has some very important implications for the ability to change the thermal tolerance characteristics of a reef-building coral association. Specifically, changes in the dominant RFLP profile that result from changes in the proportion of pre-existing symbionts is acclimation (changes in thermal behaviour without genetic change in the partners) as opposed to adaptation. As we have entered conditions that coral and coral reefs have not experienced for at least the last 400,000 years, new genetic mixes of host and symbiont are required to provide the thermal tolerances required to face these new conditions.

While convincing evidence for the ability of reef-building corals to swap their symbiotic dinoflagellate varieties is lacking, evidence to the contrary is building. Goulet and Coffroth (2002) studied the variation in the identity of symbiotic dinoflagellates in the octocoral *Plexaura kuna* over 10 years multilocus DNA fingerprinting, which is able to distinguish the genotype of individual populations of symbiotic dinoflagellates that have presumably originated from a single cell within the hosts. While the dinoflagellate fingerprints varied extensively between colonies of *P. kuna*, they did not change in any of the 21 colonies sampled frequently over 10 years. Change also did not occur after colonies bleached during episodes of elevated temperature. Eight colonies *P. kuna* sampled before and after this event in 1995 retained their unique zooxanthella DNA fingerprint.

While similar studies remain to be done for reef-building corals, techniques using the precision of multilocus DNA fingerprinting are required if assumption 4 of the ABH ("Bleaching provides an opportunity for the host to be repopulated with a different type of partner.", Ware et al., 1996) is to supported. Other aspects of the biology of symbiosis do not suggest that rapid change in symbiotic partners is possible. Weis et al. (2001) have demonstrated that symbiotic dinoflagellates from other coral species usually result in ineffective establishment of a new symbiosis compared to that of the native symbiont. Similar results have been observed for other symbiotic hosts (Trench, 1979). Given the complex nature of endosymbiosis, it is perhaps not surprising that symbionts that have the complex and specific characteristics required to form an effective symbiosis plus a higher thermal tolerance are not easily available in the environment.

There is evidence that hosts may associate with new varieties of symbiotic dinoflagellates in longer time frames that those involved in coral bleaching. For example, RFLP genotypes of symbiotic dinoflagellates that are normally associated with foraminifera have been found as the symbiotic dinoflagellates of some corals at high latitude (e.g. Rodriguez-Lanetty et al., 2001). The required observation that hosts can swap their symbionts within the ecological (short) time frame of a bleaching event has not been observed. Again, the simple yet compelling observation that mass bleaching events are becoming more intense and widespread as opposed to becoming diminished over time suggests that this strategy is not particularly potent in shaping the resistance of corals and their symbiotic dinoflagellates to future increases in sea temperature. This observation also suggests that coral evolution is slow relative to climate change and that other processes such as the reassortment of genotypes geographically (Hoegh-Guldberg, 1999) is not keeping pace with the current extremely high rate of climate change.

8. Ecological Ramifications of Climate Change on Coral Reefs

While the linkages between global change, thermal stress and coral bleaching have been largely understood, comprehension of the ecological ramifications of these changes is in its infancy. Many organisms are completely dependent on corals for habitat and food (Fig. 6) while others are not. This difference suggests radically different pathways under scenarios of global change in which coral became scarce on coral reefs. Those organisms that are completely dependent on corals for food and shelter would be expected to under go a major contraction as coral populations dwindle. Organisms that are associated with coral in more facultative ways, on the other hand, might be expected to be less affected. Several studies already support this proposal.

The Orange-spotted filefish (*Oxymonacanthus longirostris*, Fig. 6), a coral obligate, rapidly disappeared from Okinawan reefs after the 1998 bleaching event (Kokita and Nakazona, 2001). This particular species like many other species such as butterflyfish and angelfish requires coral for food, larval settlement and shelter. Removing this resource immediately impacts the numbers of individuals within an area. Similarly, the loss of coral has direct effects on obligatory coral associates (principally trapezoid crabs and Pontoniine shrimps) that live obligatorily with corals (Glynn et al., 1985; Glynn and D'Croz, 1990; Phillips, 2002). Other organisms associated with coral reefs may stand to benefit. Herbivorous fish populations appear to have increased after the 1998 mass bleaching event on Tanzanian reef systems (Lindahl et al., 2001). Similar conclusions have been seen at other sites by Chabanet (2002). Our understanding of the relationships between organisms on coral reefs is relatively scant, and hence our ability to project how changes in coral cover will impact overall species diversity and community structure on coral reefs is currently limited and should be the focus of future studies.

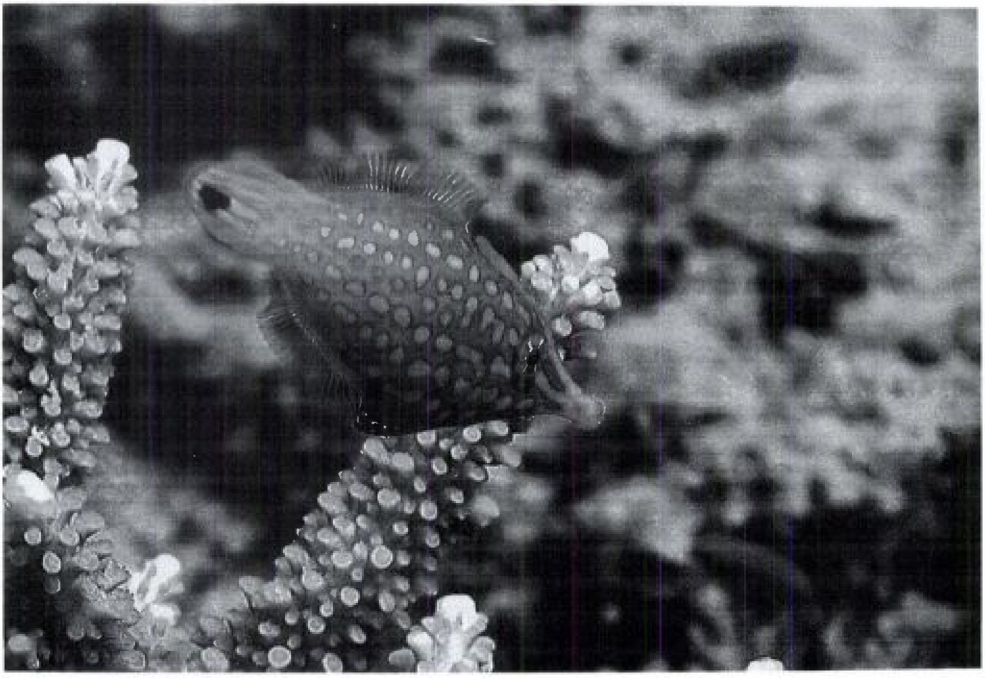

Figure 6. The loss of coral populations directly affects many species that live in a tight association with corals. The Orange spotted filefish is one example – in 1998 it was recorded to undergo a massive reduction in numbers as coral colonies were removed from corals reefs in Okinawa (Kokita and Nakazono, 2001).

Much of the preceding discussion has focused on changes and mortality of corals after experiencing thermal and light stress. Ecological ramifications can be felt, however, from changes to growth and reproductive rates of corals which are all severely inhibited by sub-lethal thermal stresses (Goreau and Macfarlane, 1990; Leder et al., 1991; Szmant and Grassman, 1990; Ward et al., 2001; Michalek-Wagner and Willis, 2001). Growing evidence also supports the notion that thermal and other stresses disrupt the delicate microbial communities on the surface of corals leading to disease. Coral diseases represent one of the major threats now for Caribbean reef systems, and have been documented to remove entire communities of corals, events which appear to be unique in the affected regions for at least the last 3,000 years (Aronson and Precht, 1997; Aronson et al., 2000). The dramatic sudden rise of diseases within corals over the past 30 years have many speculating that climate change (on top of the many other human derived stresses) is causing a major shift in the susceptibility of corals (Harvell et al., 1999, 2002).

If our understanding of the ecological changes that stem from the loss of corals is poor at present, then our understanding of the social and economic ramifications of these changes is practically non-existent by comparison. If changes in benthic structure mean that reefs are less appealing to tourists and that they support less harvestable fish and invertebrates, how will the societies that depend on these resources be impacted? This type of question, while all important, has been the focus of few studies. In Australia, for example, consideration of the main drivers for the economics of the Great Barrier Reef region reveals some chilling implications for major international money earners if coral is largely lost from the Great Barrier Reef (Hoegh-Guldberg and Hoegh-Guldberg, 2004). With the major portion of northern Queensland, for example, depending on reef interested tourism, the loss of coral dominated reefs with the Great Barrier Reef is estimated to impact local economies between 3 and 8 billion dollars over a 19 year period. Much of what happens in this respect will depend on how coral-dependent countries like Australia respond to the challenges being presented. This, in turn, depends on more complete understanding of the sequences of changes that are likely to occur as oceans warm. The problem for developing countries may be even more severe given the dependence of many developing nations on the food and building materials provided by coral reefs along their coastlines (Hoegh-Guldberg and Hoegh-Guldberg, 2000, 2004). As with developing countries, effective action now is required to help societies adapt to the specific challenges ahead.

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