

Chapter

Coral reef disturbances

This chapter covers the principal disturbances at various levels occurring or seen as a problem in coral reefs (including non-reefal coral communities) in Japan. The disturbances seen on natural environments are often caused by combination of anthropogenic and natural causes. On coral reefs, dredging by construction works and terrestrial red soil inflows are included in the former cause to a large extent, and world-wide mass bleaching event due to modern human activities can also be included as well with high possibilities. While outbreak of *Acanthaster planci* and widespread of disease-causing sponges on corals are generally considered as the later cause, causal link with human activities still cannot be denied. A new problem has brought about accompanied by the modern economic framework, turning some rural peoples' simple, traditional lives to destructive modern living styles. In addition, a problem of garbage outflow on the sea has become a cross-border debate. We have to take these situations seriously, understand each disturbing factors, and implement concrete countermeasures toward improvement. Furthermore, it is necessary to understand these disparate-looking phenomena as total, interdependent phenomena, including social and economic aspects, and establish a comprehensive philosophy on our behavior. We should strongly be aware that the most 'threatening disturbance' is our 'resignation and disinterest' to the facing problems. It must be our duty, extending to the future, to exert an effort to achieve a good relationship with the blessing nature.

2-1

Global environmental change and coral bleaching

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1 Introduction

Many coral reef researchers around the world recorded the large-scale coral bleaching event that occurred from 1997 to 1998. Wilkinson (1998) used the Internet to monitor bleaching all over the world, and provided a record of the extent of the event. In Japan, information about the coral bleaching was communicated to the public via the website of the Japanese Coral Reef Society*¹ (Kayanne 2002).

The rapid communication of this event symbolized the age of the Internet, indicating that our use of technology to disseminate information was advancing in parallel with global environmental change. Unlike local disturbances in coral reefs, this bleaching event occurred on a large scale, within a short period. Research on the bleaching in hermatypic corals was accelerated worldwide. Surveys and research conducted in Japan resulted in many published reports on coral bleaching in that region (Research Institute for Subtropics 1999; Nature Conservation Bureau, Ministry of the Environment 2002).

This section is an overview of the status of coral reef ecosystems, one of the oldest existing ecosystems on Earth (Veron 1995), the hermatypic corals that are the keystone species of these habitats, and the current state of Japanese corals. This information has been collected from recent reports by academic societies, the media, and other sources.

2 Symbiosis between corals and zooxanthellae

Hermatypic coral (hereafter, coral) is the general name applied to those species that belong to several different groups of the phylum Cnidaria, and which contain unicellular algae in their tissues. This includes most species of the order Scleractinia, all the species of the orders Coenothecalia, Stolonifera in the Class Anthozoa, and

Milleporina in the Class Hydrozoa (Nishihira and Veron 1995).

The symbiotic algae in corals are called zooxanthellae, and are dinoflagellates (~10 μm in diameter) belonging to the genus *Symbiodinium* (Photo. 1), which lives in the gastrodermal cells of the coral polyp (Kawaguti 1944; Muscatine 1980). To summarize the symbiotic relationship, the zooxanthellae use some of the carbon dioxide generated by coral respiration for photosynthesis, and the coral utilizes glycerol etc. produced by algal photosynthesis as an energy source (Grant *et al.* 1999). The algae also use coral metabolic waste products, such as ammoniums and phosphates, as nutrients for growth. This symbiosis allows corals to flourish in oligotrophic tropical seas. The presence of zooxanthellae in coral tissue also promotes coral calcification (Hidaka 2002); therefore, this symbiosis is important for reef formation by these hermatypic or 'reef-building' corals.

There are millions of zooxanthellae in 1 cm² of the tissue surface of a coral colony. Zooxanthellae undergo daily cell divisions in the coral tissue and cells, and are discharged when they cease to function. This cycle is controlled by the interaction of corals and zooxanthellae, and the density of zooxanthellae is adjusted according to external environment parameters (Smith and Muscatine 1999).

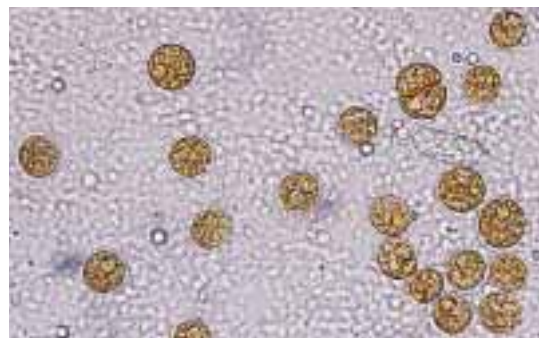


Photo. 1. Zooxanthellae (diameter ~10 μm), with some undergoing cell division.



Photo. 2. A: Healthy *Acropora hyacinthus* colony on the reef flat at 2m depth (April 1998) in front of the Sesoko Station, Tropical Biosphere Research Center, University of the Ryukyus. B: Same colony as in 2A, showing bleaching (August 1998). C: Dead colony, the surface of which is covered with algae and silt (October 1998).

3 What is coral bleaching?

Rapid environmental change causes coral stress, making it difficult to maintain the symbiotic relationship. When the symbiotic relationship collapses, zooxanthellae are eliminated from the host coral, causing 'bleaching'. Because zooxanthellae are brown in color and very abundant, a healthy coral appears to have a brown coloration (Photo. 2A). Coral tissues are thin and almost transparent, over a white calcareous skeleton, therefore when zooxanthellae are expelled, the colonies appear white and the corals are referred to as 'bleached' (Photo. 2B). This bleaching is a symptom of stress, but coral tissues can survive under bleached conditions for a limited period of time.

Extremes of environmental factors such as temperature, light, and salinity can induce bleaching (Nakano 2002a). When these factors become higher or lower than the tolerance range of the coral-zooxanthellae association, the resultant stress can lead to bleaching. Patterns of zooxanthellae expulsion vary, according to the fluctuation level of environmental stress: 1) When the change is rapid and large, coral tissues are damaged first and then zooxanthellae will be discharged (Muscatine *et al.* 1992). This is considered acute bleaching, and is a severe threat to coral health. In such cases, most of the discharged zooxanthellae are healthy. 2) When the change is comparatively gradual, there is no remarkable damage to coral tissues, however, zooxanthellae are gradually discharged. Such a discharge is considered to occur due to abnormality of cells (ie., loss of pigment and/or cell contraction) (Kuroki and van Woesik 1999). This condition is known as chronic bleaching and, although corals can survive for short periods in the bleached state, they cannot supply their energy requirements from heterotrophic sources

alone; therefore, they will become energy deficient. If this condition lasts for an extended period, corals exhaust stored energy supplies and mortality occurs (Photo. 2C).

There is a boundary between survival and mortality in bleached corals. Jones (1997) has reported that bleached corals are recoverable if the density of zooxanthellae has decreased; they are not recoverable, however, if photosynthetic pigment has been lost in conjunction with the decrease in number. While coral diseases have also been reported as potential bleaching factors, the underlying mechanisms have not yet been clarified (Kushmaro *et al.* 1996; Nakano and Yamashiro 2002).

4 Response of corals to high water temperature

There is a consensus of opinion that an abnormal rise in seawater temperatures around the world was the main cause of the large-scale bleaching of coral reefs in 1997-98 (Wilkinson 1998). Jokiel and Coles (1990) reported that a water temperature rise of as little as 1°C in summer can cause bleaching, eventually leading to coral death. Subsequent bleaching studies have indicated that the main cause of the worldwide coral bleaching in 1997-1998 was a sustained temperature that was 1-2°C higher than the average water temperature in summer.

High water temperature increases the production of toxic substances such as active oxygen within zooxanthellae (Lesser *et al.* 1990). Oxygen free radicals has an unstable charge and is in a high-energy state, which causes damage to cell organelles as well as to Photo System II, thus obstructing photosynthesis (Lesser 1997). Corals may discharge zooxanthellae in self-defense.

High water temperature reduces the amount of photosynthesis and increases the amount of respiration, which increases the carbon dioxide concentration in cells and creates a situation where bleaching readily occurs (Pecheux 1998).

The response of corals to high water temperature differs according to optical conditions, including penetration of ultraviolet rays (Glynn *et al.* 1992; Hough-Guldberg and Smith 1989). Takahashi *et al.* (2001) reported that *Acropora digitifera*, which is a dominant species on many reefs, showed photoinhibition by 250 $\mu\text{mol}/\text{m}^2/\text{s}$ or more of radiation at a water temperature of 28°C, and by 100 $\mu\text{mol}/\text{m}^2/\text{s}$ at 32°C. The recovery speed from photoinhibition rapidly decreases at temperatures above 30°C, as compared to lower temperatures. This example also shows that high temperature synergistically affect the physiological function of zooxanthellae.

As biophysical mechanisms of bleaching, corals synthesize heat shock proteins in response to high water temperature (Sharp *et al.* 1994; Black *et al.* 1995), and through adjustment of calcium ion density in cells (Fang *et al.* 1997). The synthesis of substances to absorb ultraviolet rays in corals (Glynn *et al.* 1992) seems to function as means of alleviating the effects of UV radiation.

Some genetically different clades of zooxanthellae may live together in a single coral colony (Rowan and Knowlton 1995). One of the clades may have a high tolerance to temperature stress; the coral species *Oulastrea crispata*, which contains a high density of this type of zooxanthellae (Chen *et al.* 2003), did not bleach, even during the extreme temperatures of 1998 (Nakano unpublished data). Environmental temperature extremes cause a change in the zooxanthella population composition, which, in turn, leads to different responses to bleaching. In *Goniastrea aspera*, half of the surveyed colonies bleached in 1998, but all recovered, and none of the colonies bleached in 2001 (Nakano 2002b). If different zooxanthella clades are unevenly distributed on the colony, some colonies may bleach in some parts and not others. Differences in coral inheritance types and susceptibility to bleaching at high temperatures are found in *Porites* (Edmunds 1994). Further genetic examination of these phenomena is expected in the future.

5 Impacts of bleaching on corals and coral reefs

After an improvement in environmental conditions, the coral colonies that survived the bleaching showed increased levels of infection by diseases during the recovery process (Williams and Williams 1990). In some corals, the effects of bleaching were manifested in the following reproductive season. In *Pocillopora verrucosa* colonies that recovered after bleaching in 1998, both the number of reproductive colonies and their fertilization rates decreased in 1999. Similarly, colonies of *Montipora digitata* that recovered from bleaching showed decreased numbers of oocytes and smaller testes in the reproductive period of 1999, and embryos from these colonies did not develop normally (Hirose and Hidaka 2000). Glynn and D' Croz (1990) reported that a bleached coral colony required two years for a full recovery and return to normal levels of reproductive output. The death of a parent colony from bleaching directly reduces the number of larvae in the following cohort, but even a surviving colony suffers reproductive abnormalities as a result of bleaching. In sum, bleaching, even if it is only temporary, causes reproductive problems in the coral population and/or community.

The influence of high temperature or bleaching was severe in dominant reef corals such as the fast growing arborescent *Acropora* (Loya *et al.* 2001). Therefore, the mass mortality that occurred in these corals (mainly *Acropora*), following the bleaching in 1998, influenced the entire coral reef ecosystem (Photo. 3).



Photo. 3. Reef flat in front of Cape Busena, where most of the dominant *Acropora* has died out (September 1998). Only a herbivorous fish is visible.

Corals form the basis of the coral reef ecosystem; they create structures, which, in turn, form habitats for other organisms of the coral reef community. Coral reefs that lose a dominant species show decreased coral coverage, reef productivity, and diversity. It has been found that herbivorous fish abundance increases, but that overall fish species diversity decreases (Shibuno *et al.* 1999). It has also been reported that the number of corallivorous fish decreases (Kokita and Nakazono 2001), as does the abundance of invertebrates, such as crustaceans, that are dependent on the corals (Tsuchiya 1999). The abundance of herbivorous sea urchins increased on bare substrate exposed by coral death, and excessive urchin grazing potentially increases bioerosion (Glynn 1990). Increased numbers of grazers may also remove recently settled juvenile corals, thereby impacting the initial stages of recolonization (Suefuji and van Woesik 2001).

6 Coral bleaching in Japan before 1997

Yamazato (1981) observed a comparatively large-scale coral bleaching event in the summer of 1980, on the reef flat in front of the Sesoko Station of the University of the Ryukyus. Sesoko Island is adjacent to the Motobu Peninsula, in the northern part of Okinawa Island. The bleaching was initially observed in August, and the water temperature in the moat was 30–31°C. According to fixed-point observations until next year, 100% of the *Seriatopora hystrix* and 80% of the *Stylophora pistillata* at the survey site died. However, more than 50% of the *Acropora*, *Montipora*, and *Porites* recovered, as well as all of the

Faviidae. This seems to be the country's first record of a bleaching event, and the data are presented in Table 1.

Bleaching was not observed at Ishigaki Island in 1980 (Williams and Williams 1990), but coral bleaching was observed in the Yaeyama Islands in the summer of 1983 (Kamezaki and Ui 1984). In the moat and the upper part of the reef slope (<3 m depth), many of the bleached *Acropora* and *Seriatopora* died, but many of the Faviidae and *Fungia* recovered. Bleached *Porites* were not observed at the time. The water temperature exceeded 30°C in July–August at Ishigaki Island, and warm weather maintained the high temperatures. Bleaching was also observed on the reef flat in front of the Sesoko Station in August, from which the author collected a sample of bleached Faviidae (Nakano 1984).

The Okinawa Times (August 11, evening edition) reported a bleaching event at Miyako Island in August 1986. The report stated that the water temperature exceeded the average summer water temperature of Miyako Island by 1°C from June to August. It also showed examples of bleaching observations taken from Cape Zampa on Okinawa Island and from Tokunoshima (Is.) in the Kagoshima Region during the same period. Comparatively extensive bleaching was also observed around Okinawa Island in the summer of 1986 (Tsuchiya *et al.* 1987). *Echinometra mathaei*, an echinoderm that lives in the reef flat in the southern part of Okinawa Island, also suffered high mortality, supposedly because of the high temperature (Tsuchiya *et al.* 1987).

Bleaching was observed at Ishigaki Island in 1990, according to the Nansei Regional Fisheries Research

Table 1. Regions where bleaching was recorded before 1997. ○ shows that bleaching was observed, and × that no bleaching was confirmed.

Year	Location				Reference
	Tokunoshima (Is.)	Okinawa Islands	Miyako Islands	Yaeyama Islands	
1980		○		×	Yamazato (1981); Williams and Williams (1990)
1981					
1982					
1983		○		○	Kamezaki and Ui (1984); Nakano (1984)
1984					
1985					
1986	○	○	○		Okinawa Times (August 11, 1986); Tsuchiya <i>et al.</i> (1987)
1987					
1988					
1990				○	Nansei Regional Fisheries Research Laboratory, Fisheries Agency
1991		○			Imai (1992)
1992					
1993			○	○	Department of Planning and Development, Okinawa Prefecture (1994)
1994		○		○	Fujioka (1994)
1995		○			Nakano (unpublished data)
1996		○			Nakano (unpublished data)
1997					

Laboratory of the Fisheries Agency. In the summer of 1991, bleaching was observed at Okinawa Island and around the neighboring islands of Minna, Kudaka, and Ishigaki (Imai 1992).

In the summer of 1993, a bleaching event was observed in the Miyako and Yaeyama archipelagos (Department of Planning and Development, Okinawa Prefecture 1994), and around Kerama Island (Okinawa Times, August 1, 1993).

In the summer of 1994, coral bleaching and high *Acropora* mortality were observed at Ishigaki Island and on the Motobu Peninsula of Okinawa Island (Fujioka 1994). Bleaching was also observed at Sesoko Island in 1994 and, according to a subsequent survey of *Favites chinensis* and *Platygyra ryukyuensis*, colonies that had recovered from the 1994 event, bleached again in 1995 and 1996 (Nakano unpublished data).

Records of coral bleaching before 1997 focus on Okinawa, which is partly a reflection of local community concern over the coral reefs. The extent of bleaching varied widely between islands and between regions. Bleaching damage (including partial colony damage) was confined to the area from the shallow reef flat to the upper part of the reef slope. These shallow areas were influenced by land-based impacts, as well as by temperature stress, and it is not easy to distinguish which factors were responsible for the bleaching. Environmental change in the field usually occurs as a result of many different factors. The degree of bleaching in shallow waters that are strongly influenced by nearby land (including influx of fresh water and clay sediment) will vary, therefore, between regions.

The response to high temperature and other stresses may be affected by genetic differences, even among corals of the same species (Edmunds 1994), although responses are probably more varied among different species. During local bleaching events prior to 1997-98, bleaching occurred in some colonies but not in all, even within species (Yamazato 1999); therefore, environmental factors were examined for each case individually.

7 Bleaching event after 1998, and the relation with global environmental change

In the summer of 1983, the water temperature off the coast of the Galapagos Islands remained high because of

El Niño, and most of the coral species bleached and died. Some endemic species are now thought to be extinct (Glynn *et al.* 1991).

The symbiotic relationship between animals and algae is not restricted to corals and zooxanthellae, but is also seen in many other invertebrates (Yamasu 1988). These associations were also negatively affected in the Galapagos, where a variety of other symbiotic species were bleached. Glynn (1993) suggested that such large-scale bleaching extended beyond the symbiosis between corals and zooxanthellae, and that it should be described, therefore, as a 'coral-reef bleaching event' (Photo. 4).

The large-scale bleaching event that started in the Great Barrier Reef in 1997 spread to the coral reefs of the northern hemisphere by July 1998. The main cause of the bleaching was high water temperatures. The National Oceanic and Atmospheric Administration (NOAA^{*2}, USA) superimposed images of the progressive coral reef bleaching event on satellite images of seawater temperatures, and clearly showed that the movement of a high-temperature water mass (called a 'hot spot') correlated with the progression of the bleaching (Fig. 1).

This high-temperature water mass reached Japan, causing the bleaching of coral reefs in the Ryukyu Islands and various other places (Table 2). The bleaching situation for the entire country is described in detail in Chapter 6. Large-scale bleaching of coral reefs began in Okinawa around July 1998. Many dominant coral species such as *Acropora* suffered from catastrophic damage on the west coast of Okinawa Island, resulting in decreased coral coverage and a change in community structure (Loya *et al.* 2001).

In the Ryukyu Islands, while corals suffered partial mortality in some regions, many corals recovered from bleaching in other areas. Deviation from the average water temperature, periods of high water temperatures, or the addition of factors such as light, tidal current, and turbid water may have caused these differences. In the Kerama Islands, adjacent to the west coast of Okinawa Island, the bleaching level was low and the corals recovered well. It is possible that the shallow island shelf prevented the warm water mass from reaching the shallow reefs and, therefore, the corals were not exposed to high temperatures for extended periods (Nadaoka *et al.* 2001).

A compilation of global bleaching events (Glynn 1993;



Photo. 4. Coral community in the southwest of Sesoko Island, where the dominant *Acropora* were bleached (August 1998). The large colony in the upper part of the reef is a soft coral.

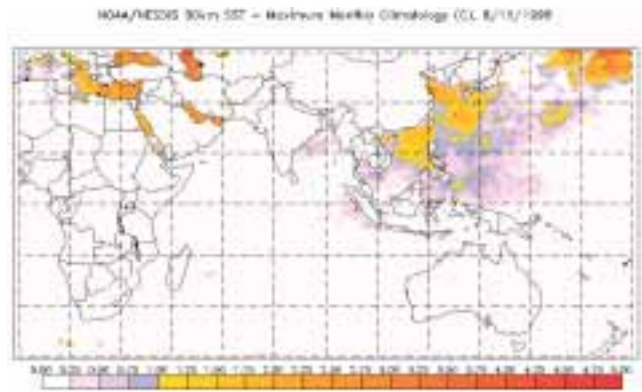


Fig. 1. Hot spot observed by satellite on August 11, 1998 by NOAA. The image shows that sea surface temperatures off the west coast of Japan (including the Ryukyu Islands) were at least 1°C above average (http://orbit-net.nesdis.no-aa.gov/orad/coral_index.html).

Table 2. Locations of bleaching in 1998.

Location	Date of login	Bleached time	Bleached depth bound (m)	Bleached species, groups	Time of died out	Died depth (m)	Died species, groups
Amakusa, Kumamoto Pref.	8.Sep.98		2-5	<i>Pocillopora</i> , etc.			
Kinko Bay, Kagoshima Pref.	4.Sep.98		2-5	tabulate <i>Acropora</i>			
Kushikino, Kagoshima Pref.	4.Sep.98	middle of Aug		<i>Acropora</i> , etc.			
Sakurajima (Is.), Kagoshima Pref.	6.Sep.98		3-5	<i>Acropora</i> , etc.			
Nakanoshima (Is.), Kagoshima Pref.	6.Sep.98			<i>Acropora</i> , etc.			
West of Tanegashima (Is.)	2.Sep.98	beginning of Aug	2-5	<i>Acropora</i> , etc.			
Yakushima (Is.)	8.Sep.98						
Kasari Bay, Amami Oshima (Is.)	9.Sep.98	middle of Aug	2-10	<i>Acropora</i> , etc.		2	<i>Acropora</i> , etc.
Tatsugou Bay, Amami Oshima (Is.)	4.Sep.98	middle of Aug	2-10	<i>Acropora</i> , etc.			
Kikaijima (Is.)	3.Sep.98						
Tokunoshima (Is.)	3.Sep.98						
Okinoerabu Is.	3.Sep.98						
Yoron Is.	3.Sep.98						
Izena Is., Iheya Is.	20.Aug.98						
Benoko, Okinawa Is.	13.Sep.98			<i>Acropora</i> , etc.			<i>Acropora</i> , etc.
North of Bisezaki, Okinawa Is.	Sep.98	beginning of Aug	2-5	<i>Acropora</i> , etc.			<i>Acropora</i> , etc.
South of Bisezaki, Okinawa Is.	7.Oct.98	middle of Aug	in moat	<i>Acropora</i> , etc.		in moat	<i>Acropora</i> , etc.
Cape Busena, Okinawa Is.	15.Sep.98	middle of Aug	≤ 30	<i>Acropora</i> , etc.		≤ 5	<i>Acropora</i> , etc.
Cape Maeda, Okinawa Is.	20.Sep.98		≤ 30	<i>Acropora</i> , etc.			<i>Acropora</i> , etc.
Ie Is.	20.Sep.98	middle of July		<i>Acropora</i> , etc.			<i>Acropora</i> , etc.
Minna Is.	Sep.98	beginning of July	≤ 30	<i>Acropora</i> , etc.	late Aug	≤ 5	<i>Acropora</i> , etc.
Sesoko Is.	Sep.98	beginning of July	≤ 30	<i>Acropora</i> , etc.	late Aug	≤ 5	<i>Acropora</i> , etc.
Kumejima (Is.)	9.Sep.98						
Akajima (Is.)	20.Sep.98		≤ 20	<i>Acropora</i> , etc.		≤ 5	<i>Acropora</i> , etc.
Nittahama, Zamami Is.	25.Sep.98		≤ 20	<i>Acropora</i> , etc.		≤ 5	<i>Acropora</i> , etc.
North of Zamami Is.	20.Sep.98			<i>Acropora</i> , etc.			
Aharen beach, Tokashiki Is.	20.Sep.98		≤ 12	<i>Acropora</i> , etc.			<i>Acropora</i> , etc.
Miyako Is.	20.Sep.98		shallows	<i>Acropora</i> , etc.		shallows	<i>Acropora</i> , etc.
Shiraho, Ishigaki Is.	20.Sep.98	middle of Aug		<i>Acropora</i> , etc.			
Kabira, Ishigaki Is.	20.Sep.98	middle of Aug	≤ 15	<i>Acropora</i> , etc.	bigginging of Sep	2-3	<i>Acropora</i> , etc.
Osaki, Ishigaki Is.	20.Sep.98	middle of Aug	5-6	<i>Acropora</i> , etc.			
Taketomi Is.	20.Sep.98		5-6	<i>Acropora</i> , etc.			

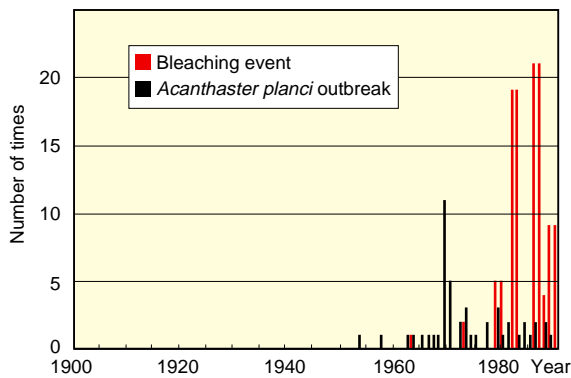


Fig. 2. Frequency of damage to corals by *Acanthaster planci* and by coral bleaching. Bleaching increased rapidly after 1980.

Fig. 2), showed that many coral communities decreased because of predation by the crown of thorns starfish (*Acanthaster planci*) and subsequent bleaching of reefs. Scientific observation of coral reefs developed rapidly with the availability of SCUBA diving technology soon after World War II. Damage from *A. planci* outbreaks started to occur frequently in the 1950s, but as the outbreaks became more significant, reef monitoring became more active. Coral reef bleaching was initially observed in the latter half of the 1970s; it was previously an unknown phenomenon. Glynn was concerned about the correlation between coral bleaching and global warming as a result of human activities. He compared the situation to that of a ‘canary in a coal mine’, a method that was used in the past to detect low levels of toxic gases in mines. He proposed that coral reefs are sensitive indicators of a deteriorating global environment, and that this issue should therefore be addressed on a global scale.

Bleaching events were localized in 1993, but became global in 1998. Total coral mortality from bleaching seems to have far exceeded the mortality attributed to *A. planci* outbreaks. Computer simulations and statistical analyses have clearly indicated that the rise in seawater temperatures that played a role in the catastrophic crisis in coral reef ecosystems is strongly related to global warming (Barnett *et al.* 2001).

Coral reef bleaching was also recorded at Okinawa Island in the summer of 2001 and 2003 (Nakano 2002b; Nakano unpublished data). Fortunately, these bleaching events were not global, but were caused by the movement of a large mass of warm water around Okinawa and neighboring areas, which was clearly confirmed using satellite observation systems etc (Shimojo *et al.* 2001). Some coral

species extended their distribution range further north during periods of anomalously high water temperatures in the Kuroshio Current (Nojima 2001). It is not yet known whether these species will reproduce and establish a regional population or disappear as failed migration. Even if a new population does establish, this might constitute a very rare case. Taking evolutionary time scales into consideration, it is doubtful whether individual species can completely adjust to a new habitat if it is only suitable during short periods of anomalously high temperatures. Environmental tolerance limits may be adjusted to permit range extension, but whether the reef species can adjust quickly enough to exploit the new habitat is unlikely. How big will this crisis turn out to be for coral reef ecosystems? It is vital that we take urgent action and increase our research efforts in this area (appeal in the 1998 Japanese Coral Reef Society convention on coral bleaching).

Cited Website:

*1: <http://www.soc.nii.ac.jp/jcrs/english/index.html>

*2: http://orbit-net.nesdis.noaa.gov/orad/coral_index.html