

## CHAPTER IV

### DISCUSSION



#### 1. The 1991 Bleaching Event and Seawater Warming.

The 1991 bleaching event along the Andaman coast of Thailand coincided with the most recent bleaching episode (1989-1991) of the world in which bleaching events occurred in wide geographical areas such as Jamaica, Caymans, Bahamas and surrounding areas in Caribbean in 1989-1990 (Goreau, 1992; Williams and Bunkley-Williams, 1992; Dennis and Wicklund, 1993), Arabian Gulf and Gulf of Oman, Indian Ocean, in 1990 (Salm (1990) in Glynn 1993), Fowler Garden Banks, Gulf of Mexico in 1990-1991 (Hagman and Gittings, 1992), Key Largo, Florida (Hallock et al., 1992), Society Islands group, French Polynesia (Salvat, 1992), Samoa (Goreau, 1992) and Okinawa, Japan (Imai, 1992; Tsuchiya et al., 1992) in 1991. Thus, these all seem to be part of a new reef bleaching complex and support the forecast of Williams and Bunkley-Williams (1990). The pattern of events also seems to conform to their 1990 model of the 1979-80, 1982-83, and 1986-88 complexes. This recent bleaching complex included preceding event, major event, and following event in 1989, 1990 and 1991, respectively.

During November-December 1990, seawater temperature which did not fall as usual may account for the striking deviations of the following summer from the normal seasonal pattern with the maximum temperature nearly reaching 32 °C in late April, 1991. Increased seawater temperatures above normal mean ambient maxima (29.4 °C) were recorded 6 weeks prior to bleaching and were likely to be the major causative factor which was also corroborated in other records from past (i.e. Jaap, 1979; Yamazato, 1981; Oliver, 1985; Glynn et al, 1988; Lang et al, 1988; Williams and Bunkley-Williams, 1988,1989) to the most recent events (i.e.

Goreau, 1992; Goreau and Hayes, 1992; Hagman and Gittings, 1992; Williams and Bunkley-Williams, 1992).

Do other contributory cause for the bleaching exist? Light is another possibility since partial bleaching occurred on shaded portions of corals where exposed surfaces were fully bleached. As individual corals experienced the same warm water and especially since genotype in a coral colony is identical, the random mosaic pattern of bleaching within a coral might be attributed to some small change in environmental stresses. A heterogeneity of bleaching responses within a coral colony in which the upper and unshaded surfaces of colonies were bleached, suggesting that light exposure might play a role in this bleaching response. For example, a comparison between the downward and upward curved surfaces on massive *Porites* spp. colonies implied that the former seem likely a focus area where light intensively strikes nearly all the times of day regardless of changing in sun azimuth while the latter becomes lesser exposed and also sometimes shaded. The common incidence of bleaching on a downward curved surfaces rather than on the upward curved surfaces on coral heads could be due to the different gradient of light intensity or duration of exposure to light. Partial bleaching of affected hosts was noted in almost all of the reports of bleaching events and light in general or UV light was usually suspected as the cause and/or intensifier (Fisk and Done, 1985; Harriott, 1985; Coles and Jokiel, 1978; Jokiel, 1988; Lang et. al., 1988; Williams et al., 1987; Williams and Bunkley-Williams, 1988, 1990).

With regard to the incidences of 1987-present bleaching on the intertidal reef flats at Ko Phuket, Brown (1987) suggested that bleaching and mortality are cyclical evidences occurring at certain time during prolonged subaerial exposure on spring tides. Bleached spot or blotch on each coral colony was consistently observed facing to the west direction (author's observation) though suspecting that the prevalent stress is intense irradiances which causing photodamage (Brown and Tissier,

personal communication).

From the above information it is reasonable to state that bleaching phenomenon along the Andaman coast of Thailand was correlated with the prolonged increase in seawater temperatures. However, some doubt still remains, as the mechanism responsible to the elevation of temperatures has not been clearly described. Although several circumstances could be implicated that light was possibly served also as a synergistic stress, the suggestion is more or less conclusive since no direct supporting evidence is available.

## 2. Coral Reef Communities Responses.

### 2.1 Reef corals

From field observation and line transect assessment data, it was apparent that responses to bleaching of corals were variable both among sites and congeneric and/or species levels. For instance, even amongst the most susceptible corals of the genus *Acropora*, either less sensitive or more resistant forms were frequently found. Certain species, i.e. *Porites lutea*, *Synaraea rus*, , *Pocillopora damicornis*, *Goniopora* spp., *Montipora* spp., etc., showed difference degree of responses from normal to completely bleached even within the same site. Clearly the causes for interspecific and intraspecific differences in bleaching are complex, being related in part to geographical differences in environmental tolerances (Coles, et al, 1976) and differences in genetic composition (Jokiel and Coles, 1990), respectively.

Responses and alteration of the whole coral community within each location seem to be variable and depended, in part, upon the degree of susceptibility of the species dominant at the sites. Prior to the bleaching event, the reef at PMBC was covered predominantly by branching *Acropora* spp., particularly *A. formosa*. These corals were the most susceptible to bleaching with respect to the rapidity of the effect and

high mortality. Similar results were recorded elsewhere during field observation and also reported in other studies, both in experimental work (Jokiel and Coles, 1974) and in bleaching events observed in the field (Yamazato, 1981; Glynn, 1983; Fisk and Done, 1985; Brown and Suharsono, 1990; Salvat, 1992). The subsequent decline of *A. formosa* in the 1991 bleaching event caused marked changes in the community structure. Immediately, the reef was replaced and dominated with the extensive lawn of filamentous algae. Initial colonization by algae on a recent dead coral surface is commonly found elsewhere (e.g. Glynn, 1984, 1990; Brown and Suharsono, 1990; Goreau and Macfarlane, 1990). At the study site, substantial reduction in coral cover was accompanied by significant reductions in species richness, abundance, and diversity. However, it was noticeable that reduction in species richness was more delicate than in abundance. This might be the important key for how coral communities could be sustained through evolutionary history by the unexpected catastrophes. Oliver (1985) agreed with the proposal of Connell (1978), and suggested that bleaching phenomenon could in some cases act as an agent for the maintenance of diversity of the coral community. Selection and genetical improvement for temperature tolerance among recovery corals were suspected and are to be fully elucidated.

## 2.2 Associated organisms

Reef corals provide a habitat for a variety of temporary and permanent residents (Patton, 1976). Any changes on coral community could also affect numerous other species that depended on live coral as shelter, food and other requisites. Furthermore, their biological and ecological activities could also be modified. Several works related to coral reef bleaching, especially during the 1982-83 ENSO warming event in the eastern Pacific, have revealed circumstances that support this point of view. The densities of obligate crustacean symbionts, *Trapezia* spp. and *Alpheus lottini*, declined significantly with the deteriorating

condition of their pocilloporid coral hosts during bleaching both in the field (Glynn, 1985b) and laboratory (Glynn et al., 1985; Glynn and D'Croze, 1990). Within suffered corals, the defensive responses of the crustaceans towards *Acanthaster planci* also declined significantly and thus allowed feeding of *A. planci* on some corals that were formerly surrounded by continuous thickets of *Pocillopora* spp. (Glynn 1985a, 1990). Severe mortality of a gastropod corallivore, *Jenneria pustulata*, on Panamanian reefs in 1983 was suggested to be contributed, in part, by the sudden decline of its mainstay coral prey, *Pocillopora* spp (Glynn 1985a). Although these aspects have not been investigated during the bleaching event in the Andaman Sea, the adverse effects to obligative coral-symbionts, i.e. *Trapezia* spp. and *Alpheus* spp., may occur in similar way.

### 2.3 Local fish assemblages

At the PMBC site, quantitative assessments of fish population during 1991-1993 suggest a curious incident of indirect effect of coral reef bleaching. The disappearance of assemblages of certain apogonid fish, i.e. *Apogon compressus*, *A. fragilis*, *A. leptacanthus* and *Archamia lineolatus*, among branching *Acropora* stands is evident. Field observations at the PMBC and other sites in Phuket have revealed confinement of apogonid assemblages to certain sheltered sites over a period of several years. Its demise is probably related to an increased vulnerability of fish to predation, which also involves emigration of this fish to other colonies. On the other hand, the first appearance of territorial damselfish, *Stegastes lividus*, among dead branching *Acropora* stands is conspicuous. This species had never been observed at least during the period of 2 years before the bleaching event. The observation in October 1991, sub-adult fish (Plate VIIa) has been noticed to assemble in large numbers (possibly first cohort) among dead branching *Acropora*. Later field observation in February 1992 and census assessments in April 1992 and May 1993 indicated abundance about 160 individuals per

1,000 m<sup>2</sup> of adult-fish, and also consistently in assemblaged (Plate VIIb). It is remarkable that the appearance of *S. lividus* on the reef resulted in large part from the appear once of new suitable shelter and/or food resources of dead branching *Acropora* with filamentous algal coat that were not widely available prior to 1991. This species is one of the most aggressive territorial damselfishes and always occupies dead branching *Acropora* corals which support a coat of filamentous algae (Allen, 1975).

#### 2.4 Fouling and boring organisms

Dead coral surface not only enhanced overgrowth of filamentous algae but also provided suitable substrate for settlement and development of various fouling and boring organisms. An examination on dead bleached coral colonies revealed high diversity and abundance of these fauna (Plates VIII-XI). An important role of bioeroders for reef degradation was generally concerned (Hutchings, 1986) especially when coincide to severe disturbances (Glynn 1988b, 1990). For the present study, porosity of dead framework (principally the dead *Acropora*) extensively produced by numerous borers (Plate XII) could affect strength which facilitates additional erosion by physical forces. Frequent strong surges during SW monsoon period probably increases erosion rates and may result in a change of reef morphology.

#### 2.5 Coral recruitment (Recovery process)

The transect assessment in 1993 revealed evidence of recovery following the 1991 bleaching event. The marked increased in coral cover, coral diversity, species richness, and occurrence of colonies in 1993 indicated that the reef has substantially recovered. The recovery was contributed by both larval recruitment and regeneration from the

partially damaged colonies. With regard to the predominance of smaller size coral colonies, <5 cm, and the marked increases in both number of colonies and species richness, the recruitment is therefore seems to be the principal process of recovery. Semi-quantitative observation on new coral recruits in July 1992 (Plates XII,XIV) indicated high recruitment of juvenile corals onto dead colonies, principally dead *Acropora* branching, which could be observed about 1 year after the bleaching. Considering the overall live coral cover during 1992 and 1993, the record showed yearly rate of live coral recovery of 6.6%. Assuming the live coral cover of a good reef is 60-70%, then it would therefore take about 7-8 years for the reef to recover. Study on recolonization of a storm damaging reef at the PMBC (southern reef site), Phongsuwan (1991) reported a recovery rate of approximately 10% per year and suggested that the reef should recover to a good condition, about 70% live coral cover, in 6-7 years. Since several factors have been considered to influence recovery and recolonization of corals following natural and anthropogenic disturbances (i.e. Endean, 1976; Pearson, 1981), the ability to predict recovery of affected reefs is thus complicated. Coral settlement is influenced by both the successional process and any disturbance. Furthermore, a successful recruit also further subject to any conditioning factors influencing survival and growth. With regard to the suggestion that recruitment is a major mean of recovery of this reef. In relation to the present reef condition, there are several relevant factors and function which probably influence recruitment process, and hence recovery, which should be considered.

Following a high coral mortality from bleaching, the present condition of reef has been predominantly covered by thick mats of filamentous algae. Coral recruitment is probably impeded since an extensive development of algae is unfavorable for corals to settle and survive (Pearson, 1981). Furthermore, filamentous algae is efficient for sediment traps which is conditioned for unsuitable substratum for coral settlement (Hatcher, 1983). However, under normal condition, with the

presence of grazing activities, the algal growth and development of algal mat should be partly inhibited. At the site, the important grazer is grazing fish, i.e. parrotfishes, rabbitfishes, and surgeonfishes, of which parrotfishes (*Scarus* spp.) exhibited the highest diurnal feeding activities (e.g. 2970–4570 bites/m<sup>2</sup>/day (Satapoomin, unpublished data). Hatcher (1983) suggested that grazing serves to restrict the thickness of algal cover thus enhancing settlement and survival of certain benthic organisms, including corals. However, intense grazing pressure probably has adverse affect even though to survival of new recruits. The role of grazing fish for controlling algal abundance (Plate XV) seem to be largely pronounced but relatively be restricted to the area outside the boundary of the territorial damselfishes (i.e. *Stegastes lividus* and *S. nigricans*). There were clear evidences for maintainance and cultivation of filamentous algal lawns within the damselfishes' territories (Plate XV), resulted from the aggressive defense of its boundary to other grazing fish. The successful recruits within the defended boundary of the damselfishes may avoid grazing but, however, the failure of those recruits might also due to the competition in space with the algae.

Since the stucy site is directly exposed to the prevailing SW monsoon, the strong wind and wave might be the cause of collapsing of the dead acroporids. An extensive invading by numerous boring organism on the dead coral skeleton might further facilitate breakage of them and produced unstable substratum not suitable for coral recruitment. Survival of recruits on these surfaces is therefore inhibited. Furthermore, this reef site is also in highly turbid water and high sedimentation (Fig. 13, 14). Under these conditions survival of new coral recruits probably be affected and also growth of juvenile corals might be impaired.

From the study sites, bleaching in the summer months of 1991 resulted in rather high mortality of corals on reefs. Data derived from line transect assessment during the bleaching event at several localities in the Andaman sea showed variability in responses and alteration of



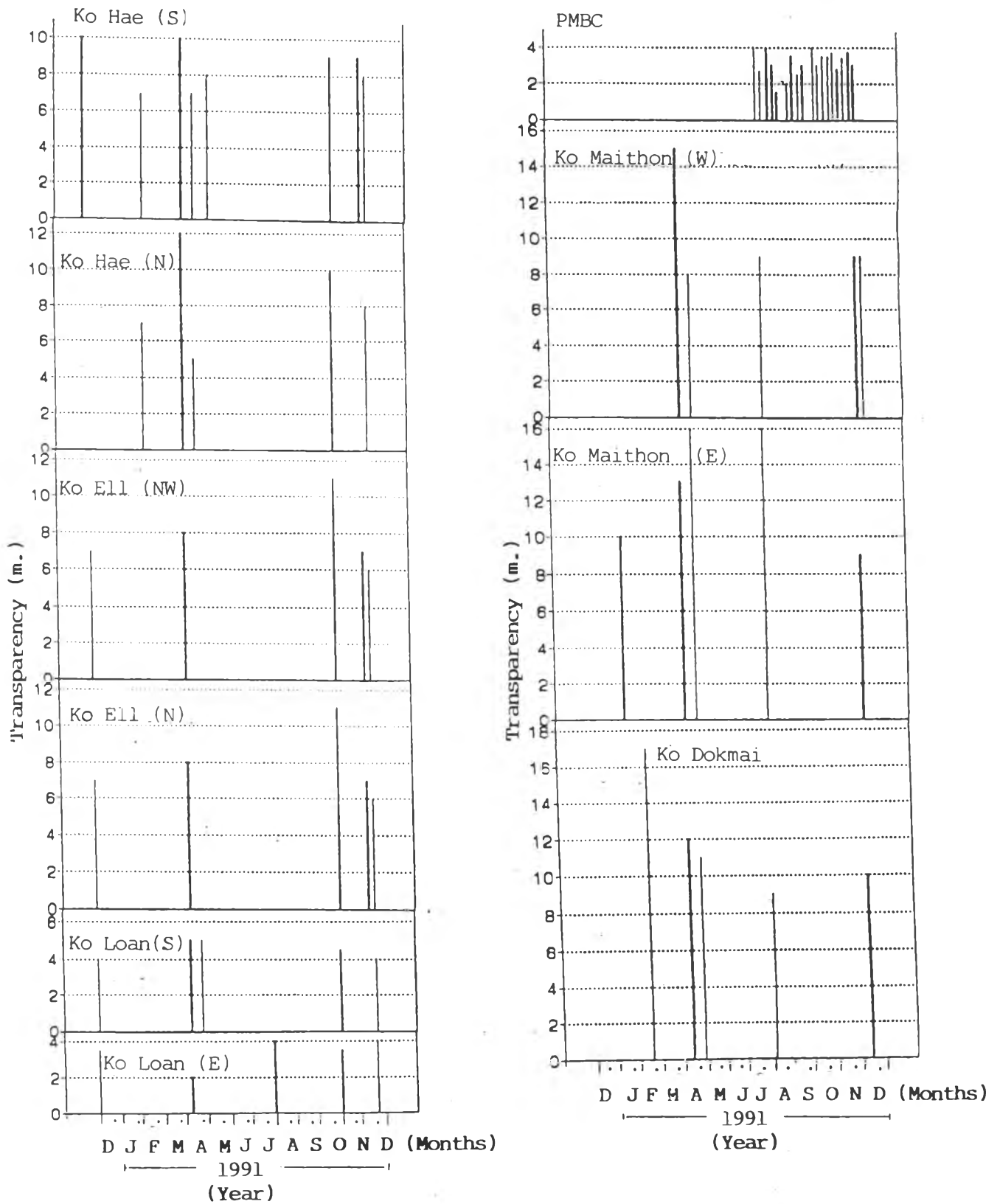


Fig. 13. Transparency (Secchi-depth) of seawater measured at several reef sites in the southern part of Ko Phuket.  
(After Phongsuwan et.al., 1992)



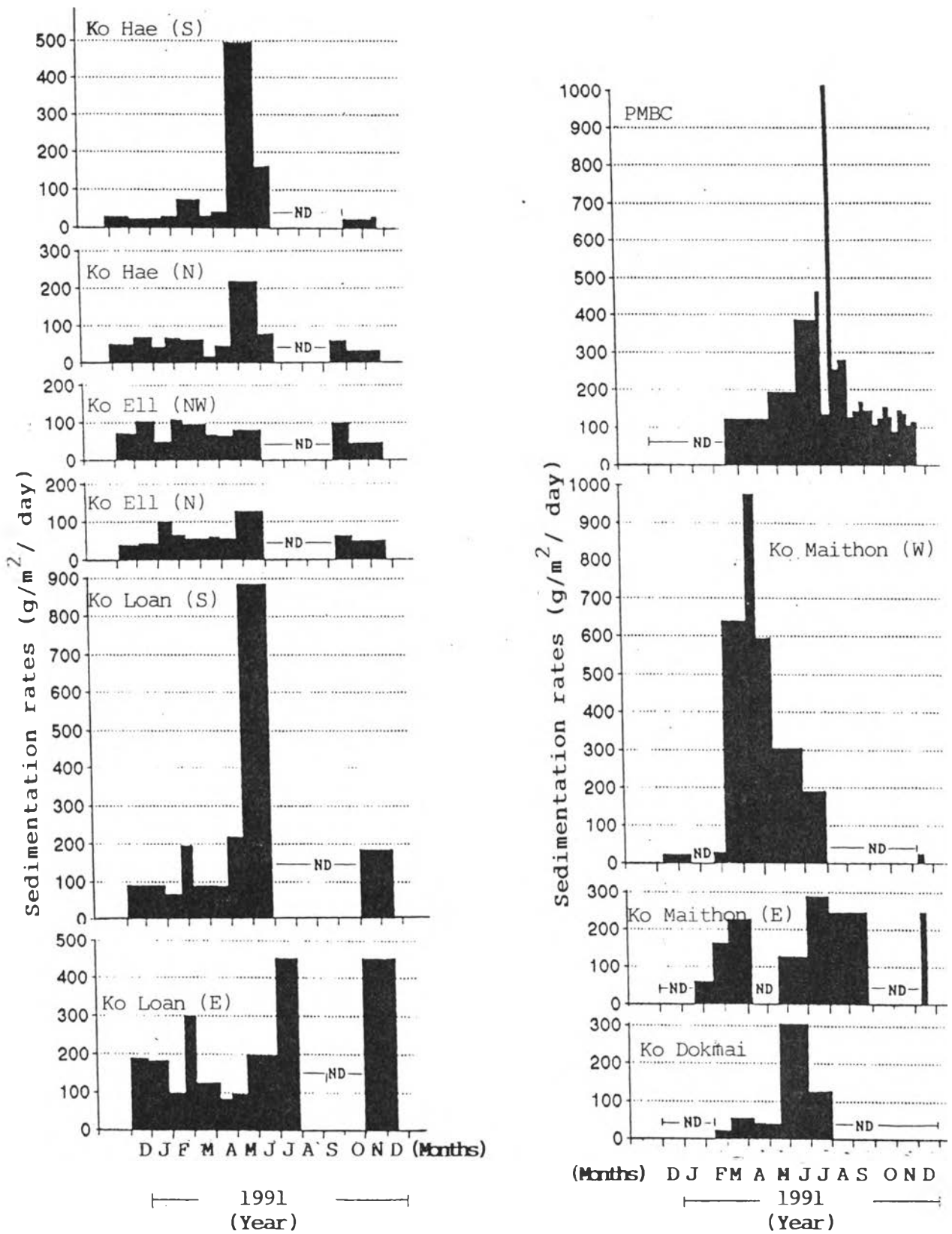


Fig. 14. Sedimentation rate measured at several reef sites in the southern part of Ko Phuket. ND= No data.  
(After Phongsuwan et al., 1992)

reefs. The PMBC and Ko Loan reef sites were among the most severely affected with respect to high percentage of coral mortality resulting from bleaching. This, however, should be treated with caution since the sites with low mortality were investigated in time-lag of about 3-4 weeks preceding the other two sites. The result will be more conclusive and reliable when repetitive transect assessments in those certain sites have been conducted and compared. Repeated assessment was done at the PMBC site which showed much higher coral mortality. Investigation at the others sites are presently under way. Other factor resulted in high mortality of bleached corals at the PMBC and Loan reef sites was likely to correlate with high turbidity of water and high sedimentation rate in the area (Phongsuwan et al, 1992). Turbidity has been suggested to complicate and intensify the 1987 bleaching in Bahamas (Bland, as cited in Williams and Bunkley-Williams, 1990) and greater bleaching was reported in areas of increased sedimentation in Puerto Rico (Morelock, as cited in Williams and Bunkley-Williams, 1990). With the loss of nutrition from zooxanthelae, feeding by polyps themselves presumably became more important. Sedimentation could result in reduction in ability to feed or diversion of coral energy resources to sediment rejection, which, therefore, resulted in weakening and more susceptibility to bleaching and then enhanced coral's death.

Coral reefs in the Andaman Sea have been continually affected by several types of disturbances such as *Acanthaster planci* infestation (Chansang, et al., 1986), sediment loading (Chansang et al., 1987), storm surge (Wongwit et al., 1989; Phongsuwan, 1991) and also tourist activities. Except for the *Acanthaster planci* infestation, most cases for severe degradation caused by those disturbances which were usually locally confined. The conspicuous coral bleaching and subsequent coral mortality that occurred during the 1991 bleaching event were among the most widespread ever recorded, and thus, seem to be the most severe disturbance of coral communities in this area.

Although it is not possible to draw conclusions about an entire reef based on just one site, the investigation performed at the PMBC reef sites, however probably be an indicative for responses on other reefs with comparable community structures and/or ambient environmental condition. Base on the base-line data of taxa componemts of coral reef in the Andaman Sea, Phongsuwan (1990) reported that the most abundant species with highest cover are *Porites lutea*, *Acropora nobilis*, *A. formosa*, and *Porites (Synaraea) rus* (see also table 13). With regard to the evidences of the severe responses and subsequence mortality of acroporids following the 1991 coral reef bleaching it might be a major decline among overall reef. The speculative point of view for the alteration of coral communities aspecially for the acroporid components may should be presume.

Further studies on the impact of bleaching on the reef community and the longterm effects on competition, predation, symbiosis, and substrate condition, all factors that can influence coral recruitments and reef recovery should also be continued.

### 3. Coral Colony Responses.

Changes of coral tissue in bleached colonies of five reef-building corals, *Lithophyllon edwardsi*, *Merulina ampliata*, *Mycedium elephantotus*, *Pectinia alcornis* and *Psammocora digitata*, have revealed valuable information about fluctuation in components of tissues during pigmentation of bleached tissues. Although the small sample size would directly reflect the high variation for most biomass parameter measurement (c.f. Appendix D), field observation during each sampling time could, however, implicate a relevant to the nature of recovery process. Visual inspection of all bleached colonies which served for any analyses were uniformly stark white at the beginning. During undergo recovery, the restoration of pigmented tissues exhibited heterogeneity

of patches over a colony. There did not appear to be any consistency to the size of the recovered zones or to the location within the colony. Within the observation period of these colonies, the recovered zones were gradually increased in size and eventually recovered to normal appearance. Translocation of the reproduced cells from the recent recovered zones to the remaining bleached zones nearly seems likely a major process of whole colony recovery. This, in turn, could help explain a rapid recovery in partially bleached corals. However, the difference in recovery degrees, such as total recovery or partial dead response, seems also to depend on the degree of susceptibility to bleaching, the amount of remnant algal cells in bleached tissue and/or potentiality of algal mitosis. Nearly whole colonies of *L. edwardsi* and *M. elephantotus* could recover to normal. In contrast *M. ampliata*, *P. alcicornis* and *P. digitata* exhibited partial dead zone 50% to 70% of the colony. Recovery of tissue biomass parameters seem to be variable among coral species. The earliest was after the 17th, for *M. elephantotus*, and as late as the 27th week, for *L. edwardsi*. The finding has suggested gradual process of tissue recovery.

In almost all cases of the present study among five coral species, bleaching resulted in reduction in some tissue components, such as 64%-95% reduction in zooxanthellae cells/cm<sup>2</sup>, 88%-99% reduction in chlorophyll-a/cm<sup>2</sup>, 54%-69% reduction in chlorophyll-a/algal cell and 43%-74% reduction in protein content/cm<sup>2</sup>. The exceptional case was found concerning the chlorophyll-a/algal cell in *M. elephantotus* which retained in relatively constant level. If the results can be generalized, the bleaching agent, such as increased temperatures, could be responsible for bleaching due to either loss of zooxanthellae or loss of chloroplast pigment or even combination of both. However, the expulsion of zooxanthellae from host tissues seemed to be common among bleached coral species. Although only increased temperature was evidently supported as a causal factor of bleaching in this study, there are evidences that both deteriorated conditions, such as zooxanthellae loss and pigment loss by

zooxanthellae were affected by high irradiance level as well. In laboratory manipulation, Hoegh-Gulberg and Smith (1985) reported that experimental bleaching of coral after exposure to high temperatures caused bleaching due to loss of zooxanthellae, but that exposure to high light intensity was due to pigment loss by the zooxanthellae. They did not find loss of zooxanthellae from high light intensities. The above findings suggested that high temperatures could be responsible for bleaching due to loss of zooxanthellae but not loss of pigment. Glynn and D'Croz (1990) found both types of bleaching even though about 50% ambient light was supplied for the temperature stress tanks. While studies on bleached corals in the field, among the common case of zooxanthellae loss, both loss by loss of zooxanthellae cell and loss of zooxanthellae pigment of chloroplast, namely chlorophyll-a and -c (Gladfelter (1988) in Glynn and D'Croz, 1990; Kleppel et al, 1989) or other accessory pigment, namely peridinin and diadinoxanthin (Kleppel et al, 1989) were always found though suspecting that high light was a contributing factor. Several other studies revealed that chlorophyll-a per zooxanthellae cell were generally inversely related to irradiance (Dustan, 1982; Muller-Parker, 1987; Battey and Porter, 1988; Lesser et al., 1990) in particular UV light (Jokiel and York, 1982; Imai, 1992). The contrast assumption might reflect differences due to species and factor initiating bleaching. Furthermore, Szmant and Gassman (1990) found both types of bleaching even among different colonies of the same coral species, *Montastrea annularis*. This point out the complication of bleaching mechanism. For the present study it could be assumed that both elevated temperatures and light intensities (even normal) have synergistically interacted and are responsible for bleaching in both loss of zooxanthellae and zooxanthella's pigment from coral, which conform to the suggestions provided by several works (i.e. Oliver, 1985; Jokiel, 1988; Jokiel and Coles, 1990). However, the susceptibility to certain stresses varied among coral species. Increased temperature was a common stress among bleached corals while light proved to be selective stress to certain species as well.

With regard to the recent concern, the complex co-evolve between cnidarians and algal symbiosis was greatly suspected for variation in bleaching. The presence of genetically different types of zooxanthellae (i.e. Blank and Trench, 1985; Rowan and Powers, 1991) with possibly different environmental tolerances in different coral host (Brown and Ogden, 1993; Glynn, 1993) is another concern which complicate the degree of bleaching in affected coral reef organisms. Algal degeneration might be expected if the strain is unable either to photoadapt to an alteration in intensities of light or to thermoadapt to temperature extreme. The susceptibly affected by most acroporid corals due to bleaching might not only to be resulted from sensitivity of the coral host but perhaps also implied sensitivity of the algal strains which selectively associated within these coral hosts. Furthermore, Sandeman (1988 in William and Bunkley-Williams, 1990) also suggested that the different patterns of bleaching could be explained by the differences in zooxanthellae in different colonies and even different parts of the same coral colony.

It is not clear if the deterioration of coral tissues, reduction in protein contents, after bleaching was due to direct coral tissue damage by the thermal stress or to a nutritional defect following expulsion of zooxanthellae. While the role of zooxanthellae in provision to their coral hosts with large quantities of organic materials has long been documented (Muscatine, 1971; Muscatine and Cernichiaro, 1969; Muscatine et al., 1981; Trench, 1971; Smith, 1979; Battey and Patton, 1984), several investigations estimated that algal translocate provides up to 100% of the host's dietary energy requirement, and may also provide materials for growth and reproduction (Muscatine et al., 1981, 1984; Davies, 1984). Furthermore, the photosynthetic capacity of the coral will be reduced in either case whether colonies lose their symbionts or whether the symbionts are retained without chlorophyll (Hayes and Bush, 1990). Based on this knowledge, it is not surprising if one find lower tissue biomass in coral which had remained bleached for a prolonged period compared to those of the normal or recovered corals (e.g. Glynn et al.

(1985), Glynn and D'Croz (1990), Szmant and Gassman (1990), and the present study, while Gates et. al. (1992) suggested that it was resulted from detachment of host cell containing zooxanthellae.

Even though there has been much attention to the most recent bleaching phenomena of several reef regions, there still be a need for extensive investigation into this phenomenon especially since no evidence exists to explain the variation and patterns of coral bleaching in the field. A greater understanding of the basic regulatory mechanism that exists between the symbiotic partners is also required. Huge gap in knowledge still remains especially insight into zooxanthellae-cnidarian hosts symbiosis, tolerance and adaptation of the couples to stress, and role of genetic variants either among zooxanthellae and/or coral in coevolution.