Mortality rates of scleractinian corals before and during a mass bleaching event

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ABSTRACT: Mass bleaching of shallow-water corals was observed at Lizard Island and at other locations on the Great Barrier Reef in early 1982. In a patch-reef community at Lizard Island, mortality rates of scleractinian corals from 4 families were higher during the period of bleaching than during the previous year. It is postulated that bleaching may be the result of penetration of high levels of UV radiation during the time of maximum annual water temperature. Mortality rates varied amongst the coral species studied, and they were generally higher in smaller colonies. The coral mortality rates recorded are comparable with those reported in similar studies of reef-flat and reef-crest habitats.

INTRODUCTION

Mortality rates are an integral part of the life-history strategies and population dynamics of scleractinian corals (Bak and Luckhurst, 1980), and have relevance to theories of community structure and diversity (Connell, 1973, 1978). There are few quantitative assessments of scleractinian coral mortality. Published estimates include those of Loya (1976a) for *Stylophora pistillata* in the Red Sea, and of Connell (1973) for a mixed species assemblage on Heron Reef. These studies were carried out predominantly in reef-flat and reef-crest habitats respectively. Potentially, such habitats are physically highly disturbed, and the high mortality rates reported might not be representative of coral communities in other habitats.

Bak and Luckhurst (1980) assessed mortality for colonies of several species over 30 cm in diameter at depths of 10 to 40 m at Curacao. The annual mortality rates of 2 to 19 % reported by them were comparable with results of Connell (1973). Bak and Engel (1979), who studied mortality of juvenile corals (<4 cm), found annual mortality rates of approximately 50 %.

Loya (1976b) suggested that the pocilloporid *Stylophora pistillata* is an r-strategist because of its high mortality and recruitment rates. In contrast, Rosen (1981) concluded that corals may generally be consi-dered as relatively K-selected, or competitors/stress-tolerators (*sensu* Grime, 1979), because of their longevity and low turnover.

In this study, mortality was assessed in 3 coral species and 1 species group. The species were selected to include a range of polyp sizes, growth forms and taxa, and their reproductive ecology was studied simultaneously (Harriott, 1983 a, b). The study was carried out on a back reef area at depths of 2 to 9 m, where physical conditions were probably intermediate between those prevailing during the studies of Connell (1973) and Bak and Luckhurst (1980).

The study period (Jan 1981 to May 1982) coincided with a period in early 1982 when widespread bleaching (= loss of zooxanthellae) was reported in shallow-water corals from many areas of the Great Barrier Reef. A similar episode of widespread bleaching and mortality of corals was reported by Glynn (1983) to have occurred in the Gulf of Chiriqui, eastern Pacific Ocean, in early 1983. The mortality of the studied species during the bleaching event was quantified and compared to that for the 1 yr period prior to the bleaching. Some causes of the bleaching are suggested.

STUDY SITE AND METHODS

The study site is a patch reef on the leeward side of the fringing reef surrounding Lizard Island and associated islands (14° 41' S, 144° 28' E). The reef is approximately 50 m diameter, with water depths of approxi-

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mately 2 m on the reef top and of 9 m at the reef base at low water.

Rates of mortality and of partial mortality were assessed for *Pocillopora damicornis* (Linnaeus), *Favia favus* (Forskal), *Lobophyllia corymbosa* (Forskal) and the *Porites lutea* (Edwards and Haime)/*australiensis* (Vaughan) group. The latter 2 species could not be separated in the field; since their distribution, abundance and reproductive ecology were very similar (Harriott, 1983a, c), it was considered valid to pool the results obtained on them for an analysis of mortality rates.

On 8 January 1981, tags were attached to the substrate close to the first 20 colonies of each species observed during a random swim over the study site. The tags were plastic 'dymo' labels attached by plastic-coated copper wire. The locations of the colonies were mapped, and the largest diameter of each colony was measured to the nearest 1 cm diameter. Diameters of tagged colonies ranged from 1 to 55 cm for *Pocillopora damicornis*, 2 to 18 cm for *Favia favus*, 3 to 40 cm for *Lobophyllia corymbosa*, and 4 to 300 cm for *Porites* species. Depth of colonies ranged from 2 to 8 m at low tide.

On 7 April, 21 August and 2 December 1981, and on 7 May 1982, the tagged colonies were relocated and recorded as dead or alive. If a colony was alive, any partial mortality (Hughes and Jackson, 1980) was recorded. If a tag could not be located, one of two options was followed: Where a colony of the same species and size was found in the mapped position, the tag was assumed to have been destroyed and the colony was retagged. The most obvious source of tag loss was fish grazing. Where no tag or colony could be found, the colony was counted as 'lost', and was not included in the analyses. Because of this factor, the

mortality estimate derived was probably an underestimate, as it is likely that some of the 'lost' colonies were in fact dead. Lost colonies were noted in 8/83 records for *Porites* colonies, 3/83 for *Pocillopora damicornis*, 3/83 for *Favia favus* and 1/82 for *Lobophyllia corymbosa*. The rate of colony loss was very low for all species except for those of *Porites*. This is attributable to the fact that *Porites* was the most abundant coral genus at the study site, and it was frequently impossible to determine whether an untagged colony at a mapped location was the original colony.

For the purposes of this study, death was defined as either tissue death, or removal of the skeleton. It is probable that in some cases, breakage of skeletons results in living fragments (Highsmith, 1980, 1982) but these were considered to be recruits from asexual reproduction rather than a continuation of the original colony. Estimates of partial mortality rates were not included in mortality estimates, but were calculated separately.

When colonies died or were lost, an equivalent number of new colonies of a similar size were tagged to keep the sample size for each time interval close to 20. Thus, the total number of observations for each species was approximately 80 (20 colonies × 4 samples periods).

For *Pocillopora damicornis* the age of each colony was estimated on the following basis: It was known from settlement experiments (Harriott, 1983c) that the diameter of a 1 yr old *P. damicornis* colony was approximately 1cm. Linear extension rates for colonies of *P. damicornis* with a diameter of 5 cm and above are approximately 2.5 cm yr^{-1} (Stephenson and Stephenson, 1933; Buddemeier and Kinzie, 1976), and extension rates are less for smaller colonies (own obs.). Using this information, a relationship between diameter and age was obtained (Table 1). From these age estimates and the calculated mortality rates, a survivorship curve was calculated.

Table 1. *Pocillopora damicornis*. Age estimated from colony diameter, annual mortality rates, and survival per 100,000 spat

Year	Range of diameter (cm)	Annual mortality (%)	No. of survivors per 100,000 spat
1	0.2 to 1	99.6	400
2	1 to 4	64	144
3	4 to 7	39	88
4	7 to 12	39	54
5	12 to 17	39	33
6	17 to 22	20	26
7	22 to 27	20	21
8	27 to 32	20	17
9	32 to 37	0	17
10	37 to 42	0	17
11	42 to 47	0	17
12	47 to 52	0	17

RESULTS

Of the colonies tagged in January 1981, 1/18 (5 %) of *Favia favus*, 2/13 (15 %) of the *Porites* species, 4/20 (20 %) of *Lobophyllia corymbosa* and 8/18 (44 %) of *Pocillopora damicornis* colonies died in the 16 mo to May 1982. In cases where a colony survived between successive sampling periods, partial mortality was recorded in 1/71 cases (1.4 %) for *Porites* species, 2/79 cases (2.5 %) for *F. favus*, 3/78 cases (3.8 %) for *L. corymbosa* and 6/66 cases (9.1 %) for *P. damicornis*. These results include partial mortality of colonies that died in subsequent sampling periods. The relative

rates of partial mortality for these species approximately parallel rates of absolute mortality.

When the number of living colonies at the beginning and end of a defined period is known, mortality for any other time period can be calculated using the following equations:

The instantaneous mortality rate (m) can be calculated from survival data for a known period of time (t_1)

$$m = \frac{\ln Nt_1 - \ln N_O}{t_1} \qquad (1)$$

The number of individuals surviving for a second period (t_2) can be calculated from m

$$Nt_2 = N_O e^{mt_2} \qquad (2)$$

Hence mortality rate can be calculated as

$$\text{Mortality} = \frac{N_O - Nt_2}{N_O} \times 100\%$$

where N_O = number of individuals at time O; Nt_1 = number of individuals living at time t_1; Nt_2 = number of individuals living at time t_2.

In this study, the length of the period between successive observations ranged from 3 to 5 mo. For each observation period and each species, the mortality rate for a standard 4 mo period was calculated (Table 2). All species showed some variation in mortality rate over the first 3 periods, but for each species, mortality was highest in the final observation period from December 1981 to May 1982.

Some bleached corals were observed in January 1982, and extensive bleaching was noted in March 1982. Zooxanthellae were absent from large areas of tissue in coral colonies at the study study site, at nearby reefs, and at reefs near Townsville (own obs.). Many small colonies were completely bleached and subsequently died, although many larger colonies regained zooxanthellae over subsequent months and recovered completely. In the Lizard Island area, bleaching occurred almost exclusively on the upper surface of corals, generally at depths of less than 5 m, but occasionally in deeper waters where the water was clear. On branching colonies, the upper surfaces of branches were frequently bleached white, while the lower and any shaded surfaces of the same branches retained normal colouration.

In order to ascertain whether the bleaching coincided with an increase in coral mortality rate, the annual mortality rate was calculated from January 1981 to December 1981, i.e. before bleaching was observed, and from December 1981 to May 1982, i.e. during the period of bleaching. For all species, mortality was higher during the bleaching period than in the previous year: 58 % vs. 31 % for *Pocillopora damicornis*, 23 % vs. 12 % for *Lobophyllia corymbosa*, 15 % vs. 5 % for *Porites* species, and 12 % vs. 0 % for *Favia favus*. For all species pooled and for *P. damicornis*, frequencies of living and dead corals were significantly dependent on the time period (χ^2 contingency table analysis, P $[\chi^2] < 0.01$). The number of dead corals was too low for the other species to permit testing.

The rate of partial mortality was also higher during the bleaching period, e.g. for *Pocillopora damicornis* 4 of the 6 records of partial mortality occurred from December 1981 to May 1982, compared with 1,0 and 1 record in each of the other 3 sample periods.

To ascertain the relationship between mortality rate and size, colonies of each species were allotted to a size class, the range of which depended on the size range of the species, and the annual mortality rate was calculated for each size class. In general, mortality decreased with increasing size class, indicating that smaller individuals are more susceptible to mortality than larger ones (Fig. 1). For *Pocillopora damicornis* the plot was extended by including data on the mortality rate of 2 mo old spat in the field (Harriott, 1983b). The spat mortality rate of 60 % for 2 mo gives an overall annual mortality rate of 99.6 %. Similar data were not available for the other species.

Using the procedure for age determination outlined above, ages were assigned to *Pocillopora damicornis* colonies according to their sizes. Mortality-rate estimates for each size class were applied and a survivorship curve from 0 to 12 yr for 100,000 newly settled spat was calculated (Fig. 2). Despite the inherent simplifications in age determination and size-related mortality

Table 2. Standardised 4-monthly mortality rates for the 4 coral species studied during the 4 sample periods. n = sample size; M = mortality rate (%)

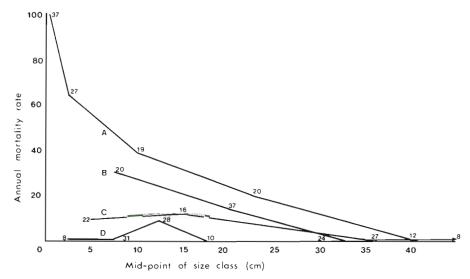| Species	Jan 81 to Apr 81		Apr 81 to Aug 81		Aug 81 to Dec 81		Dec 81 to May 82	
	n	M	n	M	n	M	n	M
Pocillopora damicornis	20	0	20	18	20	17	19	26
Lobophyllia corymbosa	20	7	21	0	21	5	19	9
Porites species	20	0	18	5	20	0	15	5
Favia favus	19	0	21	0	21	0	19	4

Fig. 1. *Pocillopora damicornis* (A), *Lobophyllia corymbosa* (B), massive *Porites* species (C), and *Favia favus* (D). Changes in mortality rate with colony size. Annual mortality rate for each size class, where size is the maximum diameter, is plotted against the mid-point of the size class. Number of observations given near each data point
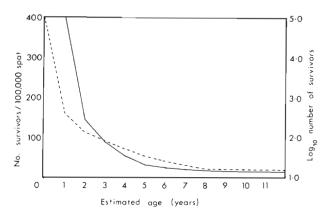

Fig. 2. *Pocillopora damicornis*. Survivorship curve from untransformed data (solid line) and on a log scale (dashed line)

(Connell, 1973; Hughes and Jackson, 1980), the method produced a good representation of a Type 3 survivorship curve, i.e. increasing survivorship with increasing age (Deevey, 1947), when results were plotted both untransformed and as a semi-log transformation (Fig. 2).

DISCUSSION

Causes of mortality

Mortality rates of the 5 scleractinian coral species showed (a) variation in magnitude amongst different species, (b) temporal variation and (c) a decrease with increasing size class.

The most commonly observed causes of mortality and partial mortality were:

(1) Physical damage as a result of wave action, bioerosion, or both, produced colonies that had been overturned or broken into fragments.

(2) Predators, in particular grazing fish and the sea star *Acanthaster planci*, were frequently seen to damage living corals. Generally, predation caused damage to only part of a colony, but death of the entire colony sometimes resulted, particularly in small colonies. Scarid grazing most commonly affected *Porites* species, leaving series of parallel teeth marks on the surface of the colonies (Glynn et al., 1972; own obs.). *Acanthaster planci* was present in low-to-moderate numbers (0 to 2 100 m^{-2}) throughout the study; they preyed on many species, but affected *Acropora* species most frequently.

(3) Tissue death by infection or unknown causes was occasionally observed, particularly in small *Pocillopora damicornis* colonies.

(4) The factors that caused mass bleaching of coral colonies between December 1981 and April 1982 resulted in increased mortality of the coral colonies.

A report of a bleaching episode of even greater magnitude than that discussed here was given by Glynn (1983). In January to April 1983, reefs in an area of about 10,000 km^2 in the Gulf of Chiriqui were bleached of zooxanthellae with subsequent high mortality (80 to 90 %). The cause of the bleaching could not be identified and a range of man-related and natural disturbances were implicated. The widespread nature and severity of these bleaching events lend importance to the search for a causative factor or factors.

Extensive loss of zooxanthellae by corals has previously been reported as a response to stress such as high
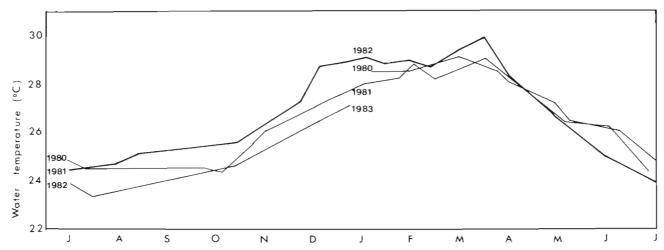
Fig. 3. Water temperature at 10 m in the open water near Lizard Island from Jan 1980 to Dec 1983. Heavy line: water temperature before and during mass bleaching event. Data supplied by the CSIRO Division of Fisheries and Oceanography, Cronulla, Australia

temperature (Shinn, 1966; Jokiel and Coles, 1974, 1977; Coles, et al., 1976; Japp, 1979), fresh-water influx (Goreau, 1964; Egana and DiSalvo, 1982), and extended darkness (Yonge and Nicholls, 1931; Franzisket, 1970).

In the Great Barrier Reef episode reported here, the stress that caused the bleaching seems to have been radiation, since the bleaching occurred only on the upper and unshaded surfaces of colonies, and since the bleaching was restricted to colonies in shallow or very clear waters. The bleaching occurred during a summer of unusually low rainfall and higher-than-average hours of sunshine (Table 3), and during the period of the year when water temperature was very high (Fig. 3). Siebeck (1981) and Jokiel and York (1982) have discussed the potentially damaging effects of UV radiation on corals, and the significance of the presence of UV blocking agent in coral tissue (Shibata, 1969). Unusually high levels of UV radiation are a possible cause of bleaching in this case, although no measurements of UV irradiance levels are available for the period and location.

Detrimental synergistic effects of environmental var-

iables have been reported by Coles and Jokiel (1978). They noted that interactions between physical factors are most important near the limits of tolerance of a given factor. The bleaching in this case occurred during the period of highest water temperature, which may in itself stress corals (e. g. Jokiel and Coles, 1974, 1977). Water temperature at Lizard Island during late 1981 and early 1982 was higher than for the same period in the other 2 yr for which data are available (Fig. 3).

Life-history strategies

The mortality rates found in this study are comparable with those reported by Loya (1976a) of about 30 % annual mortality for the pocilloporid *Stylophora pistillata*, and with those of Connell (1973) of 0 to 30 % annually in a mixed-species population. Bak and Luckhurst (1980) reported a somewhat lower mortality rate (2 to 19 %) but this may be associated with the larger size of colonies in their samples (> 30 cm diameter).

Mortality rate varied among species in the present

Table 3. Rainfall and sunshine hours in the 4 mo before and during the mass bleaching event, and the averages and/or median values for the previous 34 yr (data supplied by the Bureau of Meterology for the Townsville region)

Month	Rainfall			Hours of sunshine	
	34 yr median	34 yr average	Bleaching period	34 yr average	Bleaching period
Dec '81	62	111	61 (−45 %)	263	304 (+16 %)
Jan '82	222	305	164 (−46 %)	227	271 (+19 %)
Feb '82	301	330	182 (−45 %)	204	247 (+21 %)
Mar '82	204	233	113 (−52 %)	221	244 (+10 %)
Totals		979	520 (−47 %)	915	1066 (+17 %)

study. Mortality of *Pocillopora damicornis* was greater than that of any other species at all size classes (Fig. 2). Mortality for *Favia favus* and *Porites* species was low, that of *Lobophyllia corymbosa* intermediate. Franzisket (1970) noted that *P. verrucosa* (called *P. elegans*) exhibited a high mortality in the absence of light, relative to 3 other coral species. He correlated this high mortality with a high metabolic rate, and concluded that the species' stringent ecological requirements made it poorly adapted to withstand environmental change. Similarly, Jokiel and Coles (1974) found that *P. meandrina* showed a low tolerance for artificially raised temperatures, relative to other species, and Glynn (1976) found higher mortality rates for *P. damicornis* than for other species in both field and experimental situations. *Pocillopora* species probably expend large amounts of energy on the production of large, well-developed planulae; in a related study, *P. damicornis* was highly successful at recruitment, relative to its abundance (Harriott, 1983c). In this manner, its population can be maintained despite high mortality rates, and narrow physiological tolerances, i.e. there is a trade-off between reproductive effort, maintenance and mortality (Law, 1979).

Rosen (1981) stated that zooxanthellate corals in general are remarkable for their longevity and low turnover; that is, on an r/K life history spectrum they are relatively K selected (Stearns, 1976), and they are competitors or stress tolerators rather than ruderals (Grime, 1979). In this study, the coral species studied exhibited a range of mortality rates that varied from very high (approx. 40 % yr^{-1}) to very low (less than 5 % yr^{-1}). The corals also exhibited a range of recruitment success in a concurrent experiment (Harriott, 1983c). Thus Rosen's assumption of uniformly low recruitment and mortality in corals may be an over-simplification.

Certainly, *Pocillopora damicornis*, and the other pocilloporid *Stylophora pistillata*, have life-history features which places them on the r-selected/ ruderal extreme of a life-history spectrum (Loya, 1976 b), at least in terms of mortality rate and recruitment success. On the other hand, coral species abundant in turbid or low-light habitats are probably stress tolerant, while those with digestive dominance or overshading abilities (Lang, 1970, 1973; Connell, 1973) may be good competitors (*sensu* Grime, 1979).

Survivorship

Coral mortality rates generally decreased with increasing colony size. A similar relationship was found by both Connell (1973) and Loya (1976 a). Bak and Engel (1979) reported an annual mortality of over 50 % for corals <4 cm diameter ($^1/_3$ of colonies died in

a 6 mo period), far higher than the comparable annual mortality of an adult population (2 to 19 %, Bak and Luckhurst, 1980). Small colonies are more susceptible to most factors causing tissue death than larger ones, possibly because the area of tissue remaining following damage is too small to regenerate.

The survivorship curve for *Pocillopora damicornis* is the typical Type 3 curve of Deevey (1947) that would be expected for a marine organism producing numerous small offspring, i.e. very high mortality in juveniles and decreasing mortality rates with increasing age. Survivorship curves for the other scleractinian species studied here would be expected to follow a similar pattern if data were available for the early stages. This contrasts with the survivorship curve for the temperate coral *Balanophyllia elegans* from California (Fadlallah, 1983). *B. elegans* releases rapidly settling non-pelagic larvae with low mortality, and has a Type 2 survivorship curve, i. e. mortality rate is similar throughout the life cycle. The reproductive ecology of *B. elegans* contrasts with all other cases reported for tropical coral species (Kojis and Quinn, 1981a, b, 1982; Harriott, 1983a; Harrison et al., 1984).

Ecological consequences

The relatively high mortality established for several coral species in this study supports a concept of generally high turnover in scleractinian communities. The results of Loya (1976 a) and Connell (1973), obtained in shallow-water reef-flat habitats, are shown here to be consistent with results from deeper and more sheltered waters. A similar pattern of relatively high mortality and changes in the spatial relationships of living corals was demonstrated by Bak and Luckhurst (1980) in a physically less disturbed habitat than the one described here.

These results contribute to the small amount of baseline data on 'natural' mortality in corals that can be compared with estimates of coral mortality following some unusual phenomenon, such as a mass bleaching or pollution event. Occasional mass mortality can influence the abundance and distribution of organisms as much as, or more than, the normally encountered day-to-day mortality (Fishelson, 1973; Yamaguchi, 1975; Loya, 1976 c; Glynn, 1983). Such events might prevent long-term survival of some species in areas where their normal physiological tolerances are exceeded only occasionally, particularly if they recruit infrequently.

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